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The Hemiuridae (Digenea) of fishes from the north-east Atlantic

David I. Gibson & Rodney A. Bray

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David I. Gibson & Rodney A. Bray
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Synopsis

Keys, original descriptions, full host-records, locality data and comments on some aspects of their biology are presented for all of the hemiurid species recorded from the north-east Atlantic region. The species described are *Hemiurus appendiculatus, H. communis, H. levinseni, H. luehei, Ectenurus lepidus, Lecithocladium excisum, Glomericirrus macrouri, Lecithochirium rufoviride, L. furcolabiatum, L. fusiforme, L. musculus, Brachyphallus crenatus, Dinosoma ventrovesicularis* sp. nov. and *Synaptobothrium caudiporum*. In addition, details of the records of the larval stages from invertebrates are given, and comments are made

on the presence in the region of species of the genera *Parahemiurus* and *Dinurus*. The work includes numerous new host-records and a complete host-parasite check-list for the region.

Lecithocladium cristatum is considered a valid species, but *L. crenatum* is believed to be a questionable synonym of *L. excisum*. A great reduction in the number of the accepted species of *Lecithocladium* occurring in the Indian Ocean region is proposed. *Sterrhurus* and *Ceratotrema* are considered synonyms of *Lecithochirium*, and *L. furcolabiatum* is shown to be a valid species. *L. gravidum* is treated as a synonym of *L. rufoviride*, but *L. grandiporum* is, for the present, retained as distinct from *L. fusiforme*. *Dinosoma ventrovesicularis* sp. nov. is described from the deep-water fish *Xenodermichthys socialis*.

Introduction

This is the fourth in a series of papers on the helminth-fauna of fishes from the north-east Atlantic region (see Bray & Gibson, 1977, 1980; Gibson & Bray, 1977) and the third to deal with hemiuroid groups. The Hemiuridae is a group of digeneans which usually occurs in the stomach of marine teleosts, although forms are known from freshwater teleosts and the lung of piscivorous sea-snakes. These worms are unique in that they possess a terminal *ecsoma* or 'tail', which is capable of being retracted within the body (soma). This structure is thought to be associated with the inhospitable environment (the cardiac stomach, which these worms inhabit) in that it is believed to be a feeding organ protruded only when the pH and/or osmolarity are suitable (Gibson & Bray, 1979). The hemiurid conception and classification used in this contribution follows that of Gibson & Bray (1979).

Materials and methods

The materials and methods used in this investigation and the areas of study are as outlined by Bray & Gibson (1977). The collecting trips undertaken are as reported in previous contributions in this series, but also include: the northern North Sea and off northern Scotland aboard the MAFF RV *Cirolana* in 1979, the DAFS RV *Explorer* in 1982 and 1983 and the DAFS RV *Scotia* in 1984 (by R.A.B.); the Bay of Biscay aboard the MAFF RV *G. A. Reay* in 1980 (by R.A.B.); at Kristineberg Biological Station, Sweden, in 1976 (by D.I.G.); at the University of Tromsø, Norway, in 1980 (by D.I.G.); at the M.B.A. Laboratory, Plymouth, in 1980 (by R.A.B.); at the Marine Biological Laboratory, Helsingør, Denmark, in 1981 (by D.I.G.); at the Marine Laboratory and Huntsman Laboratory, St Andrews, New Brunswick, in 1982 and 1984, respectively (by R.A.B.); and at the Pacific Biological Station, Nanaimo, British Columbia, in 1982 (by D.I.G.).

The morphological terminology used follows that of Gibson & Bray (1979), and the fish nomenclature and classification used usually follows Hureau & Monod (1973) and Nelson (1976), respectively.

Systematic section

Family **HEMIURIDAE** Looss, 1899

Lecithochiriidae Lühe, 1901.
Dinuridae Looss, 1907.
Elytrophallidae Skrjabin & Guschanskaja, 1954.

DIAGNOSTIC FEATURES. Body usually small, but elongate. Ecsoma present, occasionally reduced or vestigial. Body-surface unspined, smooth or with annular plications; the latter occasionally being crenulate, giving a scaly appearance. Presomatic pit or ventro-cervical groove occasionally present. Oral and ventral suckers well developed; usually close together. Prepharynx absent. Pharynx well developed. Oesophagus usually short. 'Drüsenmagen' normally present. Gut-caeca terminate blindly, usually within ecsoma. Testes two; tandem, oblique or symmetrical; pre-ovarian; in hindbody. Seminal vesicle tubular, saccular or constricted into portions; muscular

or thin-walled; in fore- or hindbody. Pars prostatica of variable length; usually tubular, but occasionally vesicular; may be linked to seminal vesicle by aglandular duct. Ejaculatory duct, if present, usually short. Sinus-sac usually well developed, occasionally reduced or absent. Prostatic or ejaculatory vesicle occasionally present within sinus-sac. Hermaphroditic duct usually enclosed within sinus-sac. Permanent sinus-organ and genital atrium well developed, small or absent; temporary sinus-organ may form from hermaphroditic duct in some cases. Genital pore mid-ventral at level of oral sucker or pharynx. Ovary oval; usually entire; post-testicular. Mehlis' gland post-ovarian. Laurer's canal and canalicular or blind seminal receptacle absent. Juel's organ and uterine seminal receptacle present. Uterus coiled mainly in pre- and/or post-ovarian region of hindbody; few or no coils present in forebody; initially descending into or towards ecsoma and then ascending towards forebody. Eggs numerous; small; embryonated; rarely with a polar filament. Vitellarium varies between forms with seven tubular branches (three on one side of body, four on other) and forms with two distinct, oval masses; mainly post-ovarian. Excretory vesicle Y-shaped; arms united in forebody or not. Parasitic mainly in gut, especially stomach, of marine teleosts; occasionally present in gut of freshwater teleosts and lung of sea-snakes.

A taxonomic history of the group

Details of the taxonomic history of the hemiuroid digeneans have been reviewed by Gibson & Bray (1979). The family-group based on *Hemiurus* Rudolphi, 1809, was originally erected by Looss (1899) as a subfamily and raised to the family-level by Lühe (1901*a*). In early works on the Hemiuridae, a wide range of dissimilar forms were included in this family. Fuhrmann (1928), for example, included the Hemiurinae, Derogeninae, Dinurinae, Lecithasterinae, Sclerodistominae and Sterrhurinae (= Lecithochiriinae) within the Hemiuridae. Such a wide conception of the family has, even recently, been very popular. Workers, such as Manter & Pritchard (1960*a*) and Yamaguti (1971) have included all of these forms, with the exception of the sclerodistomines, within the Hemiuridae. Although some of these groups, such as the Derogeninae (= Halipeginae), have at various times been removed from the Hemiuridae, it was not until the works of Skrjabin & Guschanskaja (1954, 1955*a,b,* 1956) that a major change occurred. These authors retained the Hemiuridae for only the Hemiurinae and the Aphanurinae, and they recognized the Dinuridae, Lecithasteridae, Lecithochiriidae, Elytrophallidae and the Halipegidae. This system, although not accepted in its entirety, was given some support by La Rue (1957) and Joyeux & Baer (1961), who recognized the Dinuridae, Halipegidae, Lecithasteridae and Lecithochiriidae, the latter authors including only the Hemiurinae and the Prosorchiinae within the Hemiuridae. Recently, in their revision of the Hemiuroidea, Gibson & Bray (1979) have taken an intermediate position and restricted the Hemiuridae to ecsomate forms, thus recognizing the Derogenidae (= Halipegidae), Lecithasteridae and Sclerodistomidae as being distinct, and transferring the Aphanurinae to the Bunocotylidae. Within the Hemiuridae these authors accepted the following subfamilies: Hemiurinae, Dinurinae, Elytrophallinae, Glomericirrinae, Hypohepaticolinae, Lecithochiriinae, Lethadeninae, Plerurinae and Pulmoverminae. This version of the classification is followed in the present work.

Life-history and larval records

No typical hemiurid life-histories are fully known, but it is likely that they follow the typical hemiuroid pattern, as described by Køie (1978, 1979) for the derogenid *Derogenes varicus* (Müller, 1780). Embryonated eggs passed by the fish in its faeces are swallowed by gastropod molluscs and hatch in the gut, releasing the miracidium. Within the tissues of the mollusc the miracidium is transformed into a mother-sporocyst which normally gives rise to a generation of rediae (on rare occasions daughter-sporocysts). Within these parthenitae develop cystophorous cercariae, peculiar and highly modified forms possessing a tail with a caudal cyst into which the body of the worm can be withdrawn and a delivery tube through which the cercarial body is injected into the second intermediate host after the cercaria is released from the mollusc. The metacercaria, which is unencysted, usually occurs in the haemocoel of planktonic organisms, such as copepods and chaetognaths. Judging from Køie's (1978) work on *D. varicus*, it seems that

chaetognaths acquire the parasites by feeding upon infested copepods, but it is not known for certain that hemiurids cannot be acquired directly by these hosts. The piscine definitive hosts acquire these parasites either directly, in the case of young fish, small fish and filter-feeders, or indirectly by feeding upon small infested fishes. In some cases, such as some lecithochiriines, immature forms may occur encapsulated in the body-cavity of fishes which appear to act as obligatory third intermediate hosts. The complete life-history of *Lecithochirium furcolabiatum*, as deciphered by Matthews (1980, 1981*a, b*, 1982*a*), is discussed on p. 71.

Since all hemiuroids appear to have cystophorous cercariae, it is usually difficult to recognize those of hemiurids (*sensu stricto*). Many of the records of cercariae and metacercariae were published when the systematics of the group were even less well understood, and so many are questionable. All early records of ecsomate metacercariae, for example, were referred to as '*Distoma appendiculata*'; but it is unlikely that many, or indeed any, were *Hemiurus appendiculatus* (Rud., 1802). Moreover, some of the cercariae probably refer to other hemiuroid groups. Such records from the north-east Atlantic region include the following:

CYSTOPHOROUS CERCARIAE*

Cercaria appendiculata Pelseneer, 1906
(= *Derogenes varicus*)

Natica alderi – see Pelseneer (1906), Vaullegeard (1896), Dollfus (1950) and Køie (1979).

Cercaria sp. of Rees, in Dollfus (1950)

Natica alderi and *N. catenata*. Plymouth, Devon, England. Rees, in Dollfus (1950; possibly identical with *Cercaria appendiculata*).

Cercaria bunocotyle progenetica (Markowski, 1936)
(= *Bunocotyle progenetica*)

Hydrobia ulvae. English Channel and Atlantic coast of France. Deblock (1975).

Cercaria K of Rothschild (1936)

Hydrobia ulvae. Plymouth, Devon, England, and Scotland. Rothschild (1936). Possibly *Bunocotyle* according to Deblock (1975, 1981).

Cercaria sinitzini Rothschild, 1938

Hydrobia ulvae. St. John's Lake near Plymouth, Devon, England, and Scotland. Rothschild (1938*a, b*).
—— Atlantic coast of France. Deblock (1981).

Cercaria dollfusi Arvy, 1951

Philine aperta. Dinard, Ile-et-Vilaine, France. Arvy (1951).

Cercaria sp. of François, in Pelseneer (1906).

Philine aperta. Fouras, Charente-Maritimes, France. François, in Pelseneer (1906). Not *C. dollfusi* according to Arvy (1951).

Cercaria melanocystea Arvy & Gaillard, 1956

Pandora albida. Dinard, Ile-et-Vilaine, France. Arvy & Gaillard (1956).

Cercaria prenanti Arvy, 1949

Dentalium entalis. Dinard, Ile-et-Vilaine, France. Arvy (1949*a,b*, 1957).

Cercaria calliostomae Dollfus, 1923

Calliostoma zizyphinum. Roscoff, Finistère, France. Dollfus (1923).
—— Plymouth, Devon, England. Matthews (1982*a,b*).

*See also Timofeeva (1976) for forms from the Barents Sea.

Cercaria vaullegeardi Pelseneer, 1906
(= *Lecithochirium* (?) *rufoviride*)

Gibbula cinerea. Wimereux, Pas-de-Calais, France. Pelseneer (1906).
Gibbula umbilicalis. Isles Chausey, Gulf of St Malo, English Channel. Gaillard (1953).
—— Roscoff, Finistère, France. Arvy (1964).
—— Sandy Haven, Pembrokeshire, Wales. James, in Popiel (1976), Popiel (1976, 1978).

Cercaria vaullegeardi Pelseneer of Matthews
(= *Lecithochirium furcolabiatum*)

Gibbula umbilicalis. Plymouth, Devon, England. Matthews (1980, 1981*a*,*b*, 1982*b*), Gibson, Rollinson & Matthews (1985).

Cercaria filamentosa Reimer, 1971
(*?* = *Brachyphallus crenatus*)

Rissoa membranacea. Western Kattegat, Denmark. Køie (1983).

METACERCARIAE IN PLANKTON

COPEPODA

Acartia clausii [body-cavity] Plymouth Sound, Devon, England. (May, February) Lebour (1923; as *Hemiurus communis*) and (June) Lebour (1935; as *H. communis*).
—— [body-cavity and carapace] Roscoff, Finistère, France. Rose, in Dollfus (1923; not named); Rose (1925; as *Apoblema*).
—— [haemocoel] Boulogne, English Channel. Canu (1892; as *Apoblema appendiculatum*).
—— [?] Brackish water at Alnmouth, Northumberland, England. Brady (1900; as 'immature trematode').
—— [?] Firth of Clyde, Scotland. Marshall (1925; as *H. appendiculatus*).
Acartia sp. [body-cavity] North Sea (or nearby waters). Apstein (1911; as *Distomum appendiculatum*).
Calanus finmarchicus [body-cavity] North Sea (or nearby waters). Apstein (1911; as *D. appendiculatum*).
Calanus sp. [?] Firth of Clyde, Scotland. Marshall (1925; as *H. appendiculatus*).
Centropages hamatus [body-cavity] North Sea (or nearby waters). Apstein (1911; as *D. appendiculatum*).
—— [?] Kiel Bay, N Germany (February). Giesbrecht (1882; see Monticelli, 1891).
—— [?] Roscoff, Finistère, France. Rose, in Dollfus (1923; not named).
Centropages typicus [?] Roscoff, Finistère, France. Rose, in Dollfus (1923; not named).
Paracalanus parvus [body-cavity] Boulogne, English Channel. Canu (1892; as *Apoblema appendiculatum*).
—— [body-cavity] ? Helgoland, North Sea. Claus (1863; as *Monostomum*: see Steuer, 1928).
Pseudocalanus elongatus [body-cavity] North Sea (or nearby waters). Apstein (1911; as *D. appendiculatum*).
—— [?] Kiel Bay, N Germany. Pratt (1898; as *Apoblema appendiculatum*). (February) Giesbrecht (1882: see Monticelli, 1891).
Pseudocalanus sp. [cercaria observed to penetrate] Plymouth, Devon, England. Rees, in Dollfus (1950; as *Cercaria* sp. (= *Derogenes*)).
Temora longicornis [?] Roscoff, Finistère, France. Rose, in Dollfus (1923; not named).
—— [body-cavity] North Sea (or nearby waters). Apstein (1911; as *D. appendiculatum*).
Tigriopsis brevicornis [body-cavity] Wembury Bay, Devon, England. Matthews (1982*b*; as 'hemiurid metacercariae' naturally: experimental infestations with *Cercaria vaullegeardi* – see Matthews, 1981*b*, 1982*b*).
Copepod [?] Kiel Bay, N Germany. Möbius, in Willemoes-Suhm (1871; as *Distoma ocreatum*).

CIRRIPEDIA

Balanus balanoides [cercaria observed to penetrate] Plymouth, Devon, England. Rees, in Dollfus (1950; as *Cercaria* sp. (? = *Derogenes*)).

CHAETOGNATHA

Sagitta elegans [body-cavity] Northumberland, England. Meek (1928; as *Hemiurus communis*).
(?) *Sagitta rostrata* [?] Orkney Isles. Busch (1851; as *Distoma crassicaudatum* – see Lebour 1917; Dollfus, 1960*a*).
Sagitta setosa [body-cavity] Northumberland, England. Meek (1928; as *H. communis*).
(?) —— [?] In region of North Sea and English Channel (see Dollfus, 1960*a*). Busch (1851; as *D. crassicaudatum* – see Lebour, 1917; Dollfus, 1960*a*).

—— [?] Helgoland, North Sea. Leuckart & Pagenstecher (1858; as *Distoma* – see Dollfus, 1960*a*).

Sagitta sp. [gut near anus and anterior to caudal septum] St Andrews, Fife, Scotland (January, February). McIntosh (1889; as 'trematode': *?Derogenes*, according to Dollfus, 1960*a*).

—— [towards posterior part of body and elsewhere] Firth of Clyde, Scotland. Scott (1896; as 'distoma': resembles *Lecithaster*).

Spadella cephaloptera [?] Roscoff, Finistère, France (August). Dollfus (1960*a*; as (?) *Lecithaster* or *Lecithochirium*).

PROTOZOA

(?) *Noctiluca* sp. [?] Concarneau, Brittany, France. Pouchet (1883); Pouchet & de Guerne (1887).

CTENOPHORA

Pleurobrachia pileus [gut] Galway, Eire. Collected by S. Y. Yip. BM(NH) Reg. No. 1978. 12.18.1–2; as *Hemiurus* (?) *communis*. Yip (1984; as *H. communis*).

—— [?] Northern Øresund, Denmark. Køie (1983; as *Brachyphallus crenatus*).

ANNELIDA

Polygordius sp. trochophore larva [external] Plymouth, Devon, England. Lebour (1935; as *H. communis*).

FREE-LIVING METACERCARIAE

See: Giesbrecht (1882; Kiel Bay); Meek (1928; Northumberland, England); Monod, in Dollfus (1923; Concarneau, Brittany, France); and Lebour (1935; Plymouth, Devon, England).

Key to the subfamilies of the Hemiuridae in the north-east Atlantic

(In order to use this key it may be necessary to section the material.)

1 Ejaculatory (prostatic) vesicle present within sinus-sac, occasionally partly external (the vesicle should not be confused with the pars prostatica, which may be vesicular) 2
– Ejaculatory (prostatic) vesicle absent 3
2 Long, convoluted hermaphroditic duct and thin-walled permanent sinus-organ present; seminal vesicle bipartite, anterior part muscular; vitellarium two irregularly oval masses . . . . . **GLOMERICIRRINAE** (p. 54)
– Hermaphroditic duct relatively straight; permanent sinus-organ absent; seminal vesicle tubular or saccular and partitioned, usually thin-walled; vitellarium seven digitiform to oval lobes or with tendency to form two distinct, often lobed, masses; ecsoma sometimes reduced or apparently absent. . . . . **LECITHOCHIRIINAE** (p. 61)
3 Sinus-sac absent or poorly developed, when present usually of 'open'-type; seminal vesicle entirely or mainly thin-walled, usually constricted into portions; ecsoma sometimes poorly developed . . . . . **PLERURINAE** (p. 97)
– Sinus-sac present, usually well developed, occasionally small 4
4 Vitellarium two symmetrical to slightly oblique, entire or lobed masses **HEMIURINAE** (p. 6)
– Vitellarium seven distinct oval to tubular lobes. 5
5 Seminal vesicle with thick muscular wall, oval; permanent sinus-organ normally delicate and amuscular . . . . . **ELYTROPHALLINAE** (p. 45)
– Seminal vesicle thin-walled and oval, tubular or constricted into portions; permanent sinus-organ large and muscular, reduced to small papilla or apparently absent . . . . . **DINURINAE** (p. 38)

Subfamily **HEMIURINAE** Looss, 1899

DIAGNOSTIC FEATURES. Ecsoma well developed. Body-surface plicated or 'scaly' (i.e. with crenulate plications). Presomatic pit absent. Testes tandem to oblique. Seminal vesicle thin-walled, or partly or slightly muscular; bipartite or oval; in hindbody. Pars prostatica tubular; long; gland-cells occasionally delimited by membrane. Sinus-sac present; often tubular; not enclosing ejaculatory (prostatic) vesicle. Permanent sinus-organ absent, but hermaphroditic duct may be protruded to form temporary sinus-organ. Genital atrium usually small, but variable in

length. Ovary oval. Vitellarium composed of two distinct oval masses, but these may show a slight tendency towards lobation (three lobes on one mass, four on the other). Excretory arms united in forebody. Parasitic in stomach of marine teleosts.

Genus *HEMIURUS* Rudolphi, 1809

Apoblema Dujardin, 1845.
Pronopyge Looss, 1899 (see Gibson & Bray, 1979:73; Bray & Gibson, 1980: 254).
Metahemiurus Skrjabin & Guschanskaja, 1954.

DIAGNOSTIC FEATURES. Body-surface with normal plications. Seminal vesicle constricted into two portions (? occasionally three), one of which may have a thick, muscular wall.

TYPE-SPECIES. *Hemiurus appendiculatus* (Rudolphi, 1802) [by subsequent designation: Stiles & Hassal, 1898].

Key to the species of *Hemiurus* recorded from the north-east Atlantic

1 Sucker-ratio normally 1 : <1·1; distribution arctic-boreal; parasitic mainly in gadoids, but also occurs in other groups, such as salmonids and flatfishes . . . . ***H. levinseni*** (p. 25)
– Sucker-ratio normally 1 : >1·5. 2
2 Seminal vesicle relatively close to ventral sucker; distribution boreal; parasite in wide range of marine teleosts, but especially common in gadoids . . . . ***H. communis*** (p. 13)
– Seminal vesicle well posterior to ventral sucker; distribution Lusitanean; primarily parasites of clupeids 3
3 Dorsal plications reach back to level of seminal vesicle or testes (in well-preserved material); parasite of clupeids, such as herring, sprats and pilchards, and their predators (further differences are outlined in the text) . . . . . ***H. luehei*** (p. 31)
– Dorsal plications do not reach back to the level of the caecal bifurcation (except in very small specimens); parasites of *Alosa* spp. . . . . ***H. appendiculatus*** (p. 7)

Hemiurus appendiculatus (Rudolphi, 1802) Looss, 1899

? *Fasciola alosae* Hermann, 1783.
? *Fasciola clupeae* Schrank, 1788.
? *Distoma clupeae* (Schrank) Zeder, 1803.
? *Distoma clupeae rhenanae* Rudolphi, 1809.
Fasciola appendiculata Rudolphi, 1802, *nec* Frölich, 1802.
Distoma appendiculatum (Rudolphi) Rudolphi, 1809, *nec* Leidy, 1877.
Distoma appendiculatum of various authors (in part).
Distoma (Apoblema) appendiculatum (Rudolphi) Dujardin, 1845 (in part).
Apoblema appendiculatum (Rudolphi) Dujardin *sensu* Blanchard (1847).
Distoma ventricosum Rudolphi, 1819 (*nec Fasciola ventricosa* Pallas, 1774) of Wagener (1860) (in part).

TYPE-HOST AND LOCALITY. *Alosa alosa*, Griefswald on Baltic coast of East Germany.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Alosa alosa [stomach] Locality unknown. Material purchased from C. T. E. von Siebold in 1851. BM(NH) 51.7.24.180. (see Baird, 1853: 54; as *Distoma* (*Apoblema*) *appendiculatum*).
Alosa fallax [stomach] Off St. Kilda. Collected by Z. Kabata. BM(NH) 1963.6.21.44–48.
—— [stomach] SW Barra Head, Scotland (56°N, 08°W; depth 170 m; July, 1954). BM(NH) 1959.10.14.4–6. (Material of Williams, 1960: 708).
—— [stomach] Bay of Biscay (44°N, 08°W; depth 252–304 m; Jan., 1971). BM(NH) 1973.5.17.60–62. (Material of Bray, 1973: 178).
—— [stomach] Whitby, Yorkshire, England. Collected by G. A. Boxshall. BM(NH) 1976.1.5.61.
—— [?] River Severn (below Gloucester), England (May). Collected by C. R. Kennedy. BM(NH) 1983.10.19.5–6.

—— [?] Den Oever, Netherlands (Sept., 1960). Zoological Museum, Amsterdam. Cat. no. V.Pl. 372.1. (Material of Willemse, 1968: 84).
—— [?] Texel, t'Horntje, Netherlands (April, 1962). Zoological Museum, Amsterdam. Cat. no. V.Pl. 403.1. (Material of Willemse, 1968: 84).
—— [stomach] Scotland. Collected by K. MacKenzie. BM(NH) 1983.11.16.1–7.
—— [stomach] Portuguese coast (42°N, 08°W; March 1968). Laboratoria de Helminthologia Collection, Instituto Oswaldo Cruz, Rio de Janeiro. Cat. no. 30.632a–b. (Material of de Oliveira Rodrigues *et al.*, 1972: 90).
—— [stomach] Off Scarborough, North Yorkshire, England (Sept., 1976; Dec., 1976; Dec., 1977; Jan., 1978; Nov., 1978; March, 1979). Collected by D. Whittaker. BM(NH) 1982.1.19.1–3 and 1982.10.19.7–102.
—— [stomach] Estuary of River Severn off Lydney, Gloucestershire, England (May, 1979). Collected by M. V. Aprahamian. BM(NH) 1980.6.20.1–8.
—— [?] Oslofjord, Norway (1868). Collected by Esmark. Zoological Museum, Oslo. Reg. No. C.62.

(b) From elsewhere
Alosa fallax [stomach] Cairo, Egypt. Material of A. Looss. BM(NH) 1931.10.7.35–40.

(ii) NE Atlantic records from the literature
(?) *Alosa alosa* [intestine] Rennes, Brittany, France. Dujardin (1845: 420; as *Distoma* (*Apoblema*) *appendiculatum*).
(?) —— [stomach] Belgian coast. van Beneden (1871: 69; as *Distoma appendiculata*).
(?) —— [gut] River Rhine at Basle, Switzerland. Zschokke (1896: 775; as *Distoma ocreatum*).
—— [stomach] Portuguese coast (March, 1954). Tendeiro & Valdez (1955: 55).
(?) *Alosa (?) fallax* [intestine] River Rhine (May). Hermann (1783: 46; as *Fasciola alosae*).
(?) *Alosa fallax* [stomach] Belgian coast. van Beneden (1871: 68; as *Distoma appendiculata*).
—— [?] Locality not given. Odhner (1905: 349, footnote).
—— [stomach] Atlantic W of Scotland (July, 1954). Williams (1960: 708).
—— [?] Den Oever (Sept., 1960) and Texel, t'Horntje (April, 1962), Netherlands. Willemse (1968: 84).
—— [stomach] Portuguese coast (42°N, 08°W; March, 1968). de Oliveira Rodrigues *et al.* (1972: 90).
—— [stomach] SW Bay of Biscay (44°N, 08°W; depth 252–304 m; Jan., 1971). Bray (1973: 178).

Aspects of biology. The life-history of this species is not known, but it presumably follows a similar pattern to that of many other hemiurids, i.e. egg, miracidium – becoming transformed into a mother-sporocyst (in a marine mollusc), redia, cystophorus cercaria, metacercaria (in a planktonic invertebrate, especially copepods and chaetognaths), and adult (in the stomach of marine fishes, in this case *Alosa* spp.). The molluscan host is unknown. There have been many records in the literature indicating the nature of the second intermediate host, but most of these are from the late 19th and early 20th centuries, before the systematics of the genus were understood. Although most of these records were attributed to *Hemiurus* (or *Distoma*) *appendiculatus*, it is almost certain that at least the majority of these really refer to the more common species of the genus or even to other hemiurid genera (see p. 4). More recently, Hunninen & Cable (1943) claim to have found the metacercaria of *H. appendiculatus* in the copepod *Acartia* off the coast of New England; but, as discussed below, there is little concrete evidence to indicate that this parasite occurs on the western side of the North Atlantic Ocean. Indeed, we consider that it has a Lusitanean distribution (Gibson & Valtonen, 1981; Gibson, 1982, 1983), and that its distribution is limited to that of its piscine hosts. Aspects of the seasonal prevalence of this species in *Alosa fallax* in Lake Jezero, Yugoslavia, are given by Kažić (1970).

H. appendiculatus appears to be restricted to *Alosa alosa* and to *A. fallax* in the north-east Atlantic region, and it especially prevalent in the latter. These hosts are fish which enter rivers in the spring and summer to spawn in freshwater. This accounts for the records of this parasite in rivers many miles from the sea. The cause of the recent paucity of records from *A. alosa* is probably the marked decline in the numbers of this fish during the 20th century due to the pollution of many of the major European rivers. *A. fallax* has not declined to the same extent, as it does not normally penetrate nearly as far upstream.

Previous descriptions. Looss (1896: 131, as *Apoblema appendiculatum*; 1908: 103); Odhner (1905: 351, no figure); Tendeiro & Valdez (1955: 55, ignore figure). There are other descriptions;

but we have listed only the best original descriptions which we consider definitely refer to specimens of *H. appendiculatus*.

DESCRIPTION (Fig. 1). Unfortunately, we did not have available for study material collected by ourselves and fixed in glacial acetic acid or Berland's fluid. The following description is, therefore, based upon specimens many of which are rather flattened, contracted or derived from frozen hosts.

The body of this worm, although very variable, reaches a greater size than the other species of the genus in the NE Atlantic region. It is subcylindrical, narrowing terminally; but its length–width ratio depends greatly upon the extent to which the *ecsoma* is protruded (Fig. 1A & B). The latter structure can be completely withdrawn or occupy up to half of the total length of the worm. Measurements of this species are given in Table 1. The body-surface, with the exception of the ecsoma, is covered with annular *plications* ventrally and laterally. These tend to become less distinct towards the posterior end of the body-proper (soma). Dorsally, the plications tend not to occur posteriorly to the level of the intestinal bifurcation or even the pharynx; but in some cases they disappear altogether, while in some small specimens a small region of plications may occur dorsally just posterior to the ventral sucker. The *oral sucker* is ventrally subterminal and surmounted by a small pre-oral lobe. The *ventral sucker* is situated close to, and is about one and a half to two times the size of, the oral sucker, the ratio usually being in the region of 1 : 1·6–2·1.

There is no prepharynx, but a muscular, oval *pharynx* gives rise to a short, cylindrical to globular oesophagus with a tegumental lining. The oesophagus passes postero-dorsally and divides to form two short, laterally oriented ducts, which lead into distinct 'Drüsenmagen' ('glandular stomachs'). The two caeca pass back in the dorso-lateral fields from these organs and terminate blindly almost at the posterior extremity of the ecsoma.

The excretory pore occurs terminally on the ecsoma. It leads into a tubular, Y-shaped *excretory vesicle* which bifurcates at about a level just posterior to the seminal vesicle. The stem passes forward medially and slightly dorsally and the arms pass into the forebody ventro-laterally before uniting postero-dorsally to the oral sucker.

The two oval *testes* occur ventrally in the hindbody, usually about midway between the ventral sucker and the ovary; but this relationship is variable, depending upon the state of contraction. They are usually arranged obliquely, with the right testis more anteriorly situated, but they are sometimes symmetrical or their position may be reversed. The *seminal vesicle* consists of two oval, contiguous lobes, and occurs closely anterior or antero-dorsal to the testes. The proximal lobe is normally the larger, sometimes being larger than the testes; but it is thin-walled and on some occasions difficult to distinguish. The distal lobe, which leads directly into the pars prostatica, has a relatively thick, muscular wall. The pars prostatica is very long, winding in the space between the seminal vesicle and the ventral sucker, before passing into the forebody, directly or sinuously, to join the sinus-sac a short distance in front of the anterior margin of the ventral sucker (Fig. 1C). This duct is relatively dilate with a sparse, narrow covering of external gland-cells and a lining of anuclear protrusions (blebs). Spermatozoa can be seen in the lumen of the pars prostatica in one sectioned specimen. There appears to be a very short ejaculatory duct which is the small region of the male duct distal to the pars prostatica, that passes through the wall of the sinus-sac and unites with the metraterm to form an hermaphroditic duct. This union occurs just within the sinus-sac (Fig. 1C). The *sinus-sac* is tubular, straight to slightly sigmoid in the dorso-ventral plane, and possesses a thick, muscular wall. It contains the long, tubular hermaphroditic duct. In the sectioned specimen the wall of the proximal third of this duct appears to be formed from a thick layer of circular and longitudinal muscles, the middle third has a thin, smooth wall except for a small region lined with what appear to be detachable globules similar to those described below in *Hemiurus communis,* and the wall of the distal third is lined with a close-packed arrangement of tegumental, papillate structures. The latter region presumably forms a temporary sinus-organ during copulation, the papillate structures probably being an analogue of the spines which occur on the cirrus of some groups. In some fixed specimens this latter part of the hermaphroditic duct is sometimes partly everted, in some cases extending

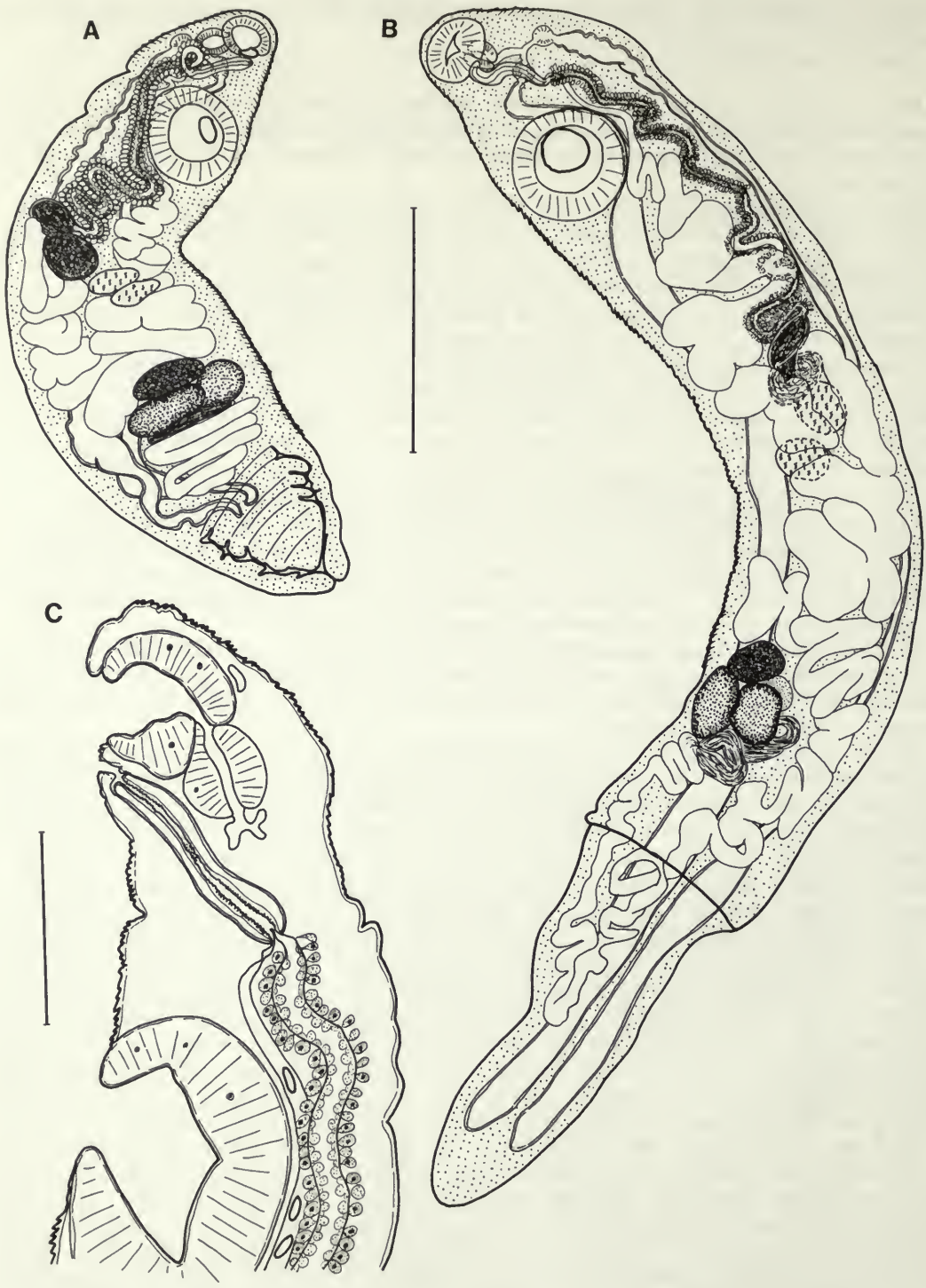


Fig. 1 *Hemiurus appendiculatus* ex *Alosa fallax*. (A,B) Entire worm, flattened and distorted; (C) Sagittal section of forebody. Scale bars: A,B 1 mm; C 200 μm.

Table 1 Measurements of *Hemiurus appendiculatus*

Authority	Material of Looss (1986) in BM(NH)	Looss (1908)	Tendeiro & Valdez (1955)	Present material
Host	*Alosa fallax*	*Alosa fallax*	*Alosa alosa*	*Alosa fallax**
Locality	River Nile at Cairo	?	Portuguese coast	NE Atlantic region
Length (mm)	1·3–4·3	3–4	3·00–5·65 plus ecsoma	0·75–6·70
Breadth (mm)	0·21–0·50†	0·4–0·5	0·76–1·29	0·20–1·00
Ecsoma (mm)	0·45–1·8	–	0·04–1·21	0·00–2·25
Ecsoma/body-length (%)	35–42	–	(1–24)	0–47
Forebody (mm)	0·15–0·27	–	0·66–1·03	0·13–0·75
Oral sucker (mm)	0·08–0·13 × 0·10–0·17†	*c.* 0·2 diam.	0·17–0·36 × 0·18–0·31	0·075–0·22 × 0·08–0·28
Ventral sucker (mm)	0·17–0·32 × 0·16–0·28†	*c.* 0·4 diam.	0·36–0·67 × 0·36–0·71	0·14–0·51 × 0·14–0·53
Sucker-ratio	1 : 1·6–1·65†	1 : 2	(1 : 1·94–2·45)	1 : 1·46–2·15
Seminal vesicle to ventral sucker/body-length (%)	12–14	–	–	9–22
Testes (mm)	?–0·13 × ?–0·13	–	0·12–0·31 × 0·10–0·32	0·02–0·27 × 0·02–0·27
Ovary (mm)	?–0·10 × ?–0·17	–	0·14–0·32 × 0·18–0·34	0·025–0·22 × 0·08–0·29
Vitelline masses (mm)	0·06–0·20 × 0·11–0·20	–	0·13–0·38 × 0·12–0·34	0·08–0·33 × 0·04–0·25
Eggs (μm)	22 × 10	20–23 × 10–12	18–24 × 10–12	18–27 × 8–12 (USUALLY 22–24 × 10)

Measurements in parentheses are calculated from figures.
*Includes one specimen from *Alosa alosa*.
†Measurements from specimen mounted laterally.

through the genital pore. There is a small genital atrium which opens to the exterior mid-ventrally close to the base of the ventral margin of the oral sucker.

The subglobular *ovary* is present in a position between the middle and posterior end of the soma, or even within the ecsoma, its position depending upon the extent of the contraction of the body and the extent to which ecsoma is evaginated. It is well separated from the testes by loops of the uterus. The ovarian complex is very compact and the ducts are very difficult to follow in our sectioned specimen. A well-developed Juel's organ, Mehlis' gland and uterine seminal receptacle are, however, clearly visible in sections postero-dorsal to the ovary. The arrangement of these organs and the associated ducts is presumably similar to that which we have described in detail for *Hemiurus levinseni* (see p. 30). The uterine seminal receptacle is large and winds posteriorly to the vitellarium. The *uterus* continues back, following a convoluted course into the ecsoma, and, when the latter is evaginated, often reaches into the posterior half and occasionally into the posterior third of this organ. It then reflexes and winds anteriorly, coiling especially between the ovary and the ventral sucker, where it is very broad, and particularly in the dorsal field and posterior to the testes where it fills much of the available space. At the level of the ventral sucker the uterus narrows, and runs forward directly or sinuously to the base of the sinus-sac. Immediately prior to its entry into the wall of the sinus-sac, there is some evidence in our sectioned specimen that there may be a slight constriction caused by a sphincter muscle (Fig. 1C), which forms a small vesicle

similar to the one described in *Hemiurus communis* (see p. 24). The numerous small eggs which fill much of the uterus are operculate and lack spines or filaments. The *vitellarium* is composed of two oval masses which lie symmetrically positioned, ventral and immediately posterior to the ovary. In juvenile forms, however, these vitelline masses can be distinctly three- and four-lobed.

DISCUSSION *Hemiurus appendiculatus* was probably first reported, as *Fasciola alosae*, by Hermann (1783) in *Alosa fallax* (i.e. a shad which was not *A. alosa*) from the River Rhine. These specimens appear to have be re-named *Fasciola clupeae* by Schrank (1788) and *Distoma clupeae rhenanae* by Rudolphi (1809). The latter author did indicate, however, that this species was probably a synonym of *Distoma appendiculatum*, which he had earlier (1802) described, as *Fasciola appendiculata*, from *Alosa alosa* in the Baltic Sea. More recent authors have accepted this synonymy, but have retained the specific appellation *appendiculatus* because, whereas the descriptions of both *Fasciola alosae* and *F. appendiculata* are meagre, Rudolphi's type-specimens have been available for study in the Berlin Museum.

Unfortunately, prior to the work of Odhner (1905), all of the currently accepted species of *Hemiurus* from the north-east Atlantic region (with the exception of *H. ocreatus* (= *H. luehei*) and certain other hemiurids) tended to be recorded under the specific name *appendiculatus*. Odhner recognized the four species, *H. appendiculatus*, *H. communis*, *H. levinseni* and *H. luehei*, which are included in the present work.* The initial use of the name *Hemiurus appendiculatus* (usually under the generic names *Distoma* and *Apoblema*) in the early literature for this complex of species has caused a certain amount of confusion for later workers. Many authors appear to have ignored the comments of Looss (1908), who suggested that *H. appendiculatus* occurs only in *Alosa fallax*, and have recorded it in a whole range of hosts. Certainly its morphological similarity with *H. luehei* is partly responsible for this, as is the basic similarity in gross morphology of many of the hemiurids. As an example, Willemse (1968) recorded *H. appendiculatus* from *Salmo trutta*, *Osmerus eperlanus* and *Gasterosteus aculeatus* in addition to *Alosa fallax*. We have examined this material and, although the specimens from *A. fallax* are indeed *H. appendiculatus*, the remainder of the material was *Brachyphallus crenatus* (Rud., 1802) with the exception of a single specimen from *G. aculeatus* which was *Lecithaster gibbosus* (Rud., 1802). It is also possible that Linton (1940), who described *H. appendiculatus* from *Alosa* [*Pomolobus*] spp. and several other hosts from off the coast of New England, might also have misled other North American workers into believing that this species occurs on the western side of the North Atlantic (our specimens from *Alosa* [= *Pomolobus*] *pseudoharengus* in Passamaquoddy Bay, New Brunswick, are *H. levinseni* – see p. 26). We can find no concrete evidence that this species occurs outside European or North African (mainly Mediterranean) waters, both in the sea and freshwater, or in hosts other than *Alosa fallax* and, less frequently, *A. alosa*. The records from *Alosa* [= *Caspialosa*] spp. in the Black Sea should be carefully reconsidered in the light of our studies from the NE Atlantic. To return to Linton's record, the nature of the seminal vesicle and the shortness of the pars prostatica in his figures suggests that his material may have been *Parahemiurus merus* (Linton, 1910). On the other hand, the host-range is more similar to *H. luehei* than to *H. appendiculatus*; but, except for a record of Linton (1901) which we hesitate to accept, there are no records of *H. luehei* on the western side of the North Atlantic. Evidence from our own collections from the Atlantic coast of Canada (see Bray, 1979) and from the literature indicates that *Hemiurus levinseni* and *Brachyphallus crenatus* are the most widespread hemiurids in the region. In addition, material labelled *H. appendiculatus* from off Bermuda, which we have examined, is in our opinion a species of *Parahemiurus* Vaz & Pereira, 1930.

As suggested by Bray (1973), the figure of *H. appendiculatus* from *Alosa fallax* off the coast of Portugal given by de Oliveira Rodrigues *et al.* (1972) differs somewhat from the usually accepted morphology of this species, especially in the nature and position of the seminal vesicle and pars

*Prior to Odhner's work, Wagener (1860) had recognized that a complex of ecsomate worms were known under the specific appellation *appendiculatum*. He split this into four species, one of which he referred to as *Distoma ventricosum* Rudolphi (in actual fact *D. ventricosum* Rud., 1819, is the type-species of *Pronoprymna* Poche, 1926 – see Bray & Gibson, 1980). *D. ventricosum* of Wagener appears to be a composite of the modern concepts of *H. appendiculatus* and *H. luehei*.

prostatica. We initially thought that this material might belong to a species of *Parahemiurus*; but, through the kindness of Dr de Oliveira Rodrigues, we have examined some of this material and can confirm that they are typical specimens of *H. appendiculatus*.

Hemiurus communis Odhner, 1905*

Distoma appendiculatum (Rudolphi, 1802) of authors (in part).
Distoma (*Apoblema*) *appendiculatum* (Rudolphi) Dujardin, 1845 (in part).
Apoblema appendiculatum (Rudolphi) Dujardin of authors (in part).
Distoma ocreatum Molin of Olsson (1868) (in part).
Hemiurus luehei of Duniec (1980).

TYPE-HOST AND LOCALITY. *Salmo trutta*,** off Kristineberg, west coast of Sweden.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Ammodytes marinus [stomach] Aberdeen, Scotland (Oct., 1973). BM(NH) 1983.11.3.2.
Argentina sphyraena [?] Firth of Clyde, Scotland. BM(NH) 1966.9.6.26–30. (Material of Halliday, in Scott, 1969: 882).
Aspitrigla cuculus [stomach] Plymouth, Devon, England (May, 1972). BM(NH) 1983.11.3.6–25.
—— [stomach] Off west Scotland (57°N, 09°W; depth 120 m; Oct., 1978). BM(NH) 1983.11.3.4.
—— [stomach] N of Scotland (59°N, 04°W; depth 81 m; June, 1982). BM(NH) 1983.11.3.5.
Ciliata mustela [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1983.11.3.6–25.
Conger conger [stomach] Off Banff, Scotland (45°N, 02°W; depth 152–186 m; July, 1976). BM(NH) 1983.11.3.26.
—— [stomach] Plymouth, Devon, England (May, 1932). BM(NH) 1932.11.29.1–6. (Material of Baylis & Jones, 1933: 631).
Cyclopterus lumpus [stomach] Aberdeen, Scotland. BM(NH) 1983.11.3.27.
Dicentrarchus labrax [stomach] Plymouth, Devon, England (Oct., 1972). BM(NH) 1983.11.3.28.
—— [stomach] Aberdeen, Scotland (Jan., 1964). Collected by K. MacKenzie. BM(NH) 1983.11.3.29.
Epigonus telescopus [stomach] NW of Flannan Isles (59°N, 09°W; depth 890–900 m; April, 1973). BM(NH) 1983.11.3.30.
Eutrigla gurnardus [stomach] Plymouth, Devon, England (Oct., 1972) BM(NH) 1983.11.3.31; (Oct., 1980) BM(NH) 1983.11.3.32.
—— [stomach] NNE of Flannan Isles (59°N, 07°W; depth 104–108 m; July, 1976). BM(NH) 1983.11.3.33.
—— [stomach] SE Ness Head, Scotland (58°N, 03°W; depth 62 m; May, 1984). BM(NH) 1984.7.20.68.
Gadus morhua [stomach] Öresund at Helsingør, Denmark (Aug., 1981). BM(NH) 1981.9.30.24.
—— [stomach] Aberdeen, Scotland. BM(NH) 1972.3.27.9; (Feb., 1969) BM(NH) 1983.11.3.34; (Oct., 1973) BM(NH) 1983.11.3.35–38.
—— [stomach] St. Andrews, Scotland (June, 1950). Collected by D. R. R. Burt. BM(NH) 1983.11.3.39.
—— [stomach] Off Banff, Scotland (58°N, 02°W; depth 130–160 m; July, 1976). BM(NH) 1983.11.3.40–42.
—— [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1983.11.3.43–49.
—— [stomach] Off E Scotland. (Isle of Fidra; 56°N, 03°W; depth 46 m; May, 1984) BM(NH) 1984.7.20.63; (Montrose Bank: 57°N, 02°W; depth 55 m; May, 1984) BM(NH) 1984.7.20.64.
Gaidropsarus vulgaris [stomach] Scarborough, Yorkshire, England. (Dec., 1977) BM(NH) 1983.11.3.50–52; (Jan., 1980) BM(NH) 1983.11.3.53; (Dec., 1981) BM(NH) 1983.11.3.54.
Gobius paganellus [stomach] Wembury, Plymouth, Devon, England (Oct., 1980). BM(NH) 1983.11.3.55.
Hippoglossoides platessoides [stomach] Off eastern Scotland (56°N, 02°W; depth 65 m; May, 1983). BM(NH) 1983.11.3.56.

*Dollfus (1968: 148) lists *Hemiurus serrulatus* (Müller, 1780) as a senior synonym of *H. communis*; but we have listed Müller's record as a questionable synoynm of *H. levinseni*.

**Odhner (1905) did not list the hosts of this species, but Dollfus (1960*b*) found specimens from both *Salmo trutta* and *Raniceps raninus* in Odhner's collection labelled as 'types'. Dollfus lists these as syntypes and, in addition, in a figure legend also refers to a specimen from *Myoxocephalus scorpius* as a syntype. As no distinct type-host has been put forward, we have listed it as *Salmo trutta* as Dollfus lists this host first, figures specimens from it in more detail, and because we have material from this host from the type-locality.

Hippoglossus hippoglossus [stomach] Moray Firth (58°N, 03°W; depth 84 m; June, 1982). BM(NH) 1983.11.3.57.

—— [stomach] N of Scotland (59°N, 05°W; depth 64 m; June, 1982) BM(NH) 1983.11.3.58; (59°N, 04°W; depth 55 m; June, 1982) BM(NH) 1983.11.3.59.

Hoplostethus atlanticus [stomach] W of St. Kilda (58°N. 10°W; depth 920–980 m; April, 1973). BM(NH) 1983.11.3.56.

Hyperoplus lanceolatus [stomach] Aberdeen, Scotland (Oct., 1973). BM(NH) 1983.11.3.65–70.

Limanda limanda [stomach] Cape Wrath, Scotland (59°N, 05°W; depth 90 m; July, 1976). BM(NH) 1983.11.7.1.

—— [stomach] Off Wick, Scotland (58°N, 03°W; depth 66–70 m; July, 1976). BM(NH) 1983.11.7.2.

—— [stomach] Aberdeen, Scotland (Oct., 1973). BM(NH) 1983.11.7.3–8.

—— [stomach] Moray Firth (58°N, 03°W; depth 35 m; June, 1982). BM(NH) 1982.11.7.9.

Lophius piscatorius [stomach] Plymouth, Devon, England. Collected by M. Rothschild, BM(NH) 1932.11.22.47–51; BM(NH) 1932.11.29.7–8 (Material of Baylis & Jones, 1933: 631).

—— [stomach] N of Scotland (59°N, 04°W; depth 66 m; June, 1982) BM(NH) 1983.11.7.12; Solan Bank (59°N, 05°W; depth 66 m; May, 1984) BM(NH) 1984.7.20.67.

Merlangius merlangus [stomach] Stanton Banks, W of Scotland (56°N, 08°W; depth 165 m; July, 1954) BM(NH) 1959.10.14.3 (Material of Williams, 1960: 708).

—— [stomach] Plymouth, Devon, England (May, 1932) BM(NH) 1932.11.29.9 (Material of Baylis & Jones, 1933: 631); (Oct., 1972) BM(NH) 1983.11.7.13–14.

—— [stomach] E of the Shetlands (60°N, 01°E; depth 116 m; July, 1976). BM(NH) 1983.11.7.15.

—— [stomach] Whiten Bank, N of Scotland (59°N, 05°W; depth 62–64 m; July, 1976) BM(NH) 1983.11.7.16; Pentland Firth (59°N, 02°W; depth 68 m; May, 1984) BM(NH) 1984.7.20.69.

—— [stomach] Off St. Kilda. Collected by Z. Kabata. BM(NH) 1963.6.21.39–43.

—— [stomach] Hinkley, River Severn, England (Oct., 1973). Collected by D. C. Gardner. BM(NH) 1977.2.10.1.

—— [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1983.11.7.17.

—— [?] Buchan Deeps, E of Scotland (Feb., 1963). Collected by K. MacKenzie. BM(NH) 1983.11.7.18.

Merluccius merluccius [stomach] Plymouth, Devon, England (Oct., 1972). BM(NH) 1983.11.7.19.

Molva molva [stomach] Plymouth, Devon, England. Collected by M. Rothschild, BM(NH) 1932.11.22.52; (May, 1932) BM(NH) 1932.11.28.50–54 (Material of Baylis & Jones, 1933: 631).

—— [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1983.11.7.20–33.

—— [stomach] NE of Scotland (57°N, 01°W; depth 67 m; June, 1982). BM(NH) 1983.11.7.34.

Myoxocephalus scorpius [stomach] Aberdeen, Scotland (Oct., 1973). BM(NH) 1983.11.7.35.

Pagellus bogareveo [stomach] Plymouth, Devon, England (May, 1972). BM(NH) 1983.11.7.36–37; (Oct., 1972) BM(NH) 1983.11.7.38.

Phycis blennoides [stomach] WSW of Barra Head, Scotland (57°N, 09°W; depth 656–665 m; April, 1973). BM(NH) 1983.11.7.39.

Platichthys flesus [stomach] Aberdeen, Scotland. (March, 1969) BM(NH) 1983.11.7.40; (Oct., 1973) BM(NH) 1983.11.7.41.

—— [stomach] Ythan estuary, Aberdeenshire, Scotland (all year round). BM(NH) 1983.11.7.42–56 (Material of Gibson, 1971).

—— [stomach] Plymouth, Devon, England. BM(NH) 1972.3.27.8; (May, 1972) BM(NH) 1983.11.9.1.

—— [stomach] Loch Ewe, Scotland. BM(NH) 1983.11.9.2.

Pollachius pollachius [stomach] Northern North Sea. (59°N, 02°E; depth 98 m; May, 1983) BM(NH) 1983.11.9.3; (59°N, 06°W; depth 84 m; May, 1984) BM(NH) 1984.7.20.65.

Pollachius virens [stomach] Aberdeen, Scotland (Oct., 1973). BM(NH) 1983.11.9.4–40.

—— [stomach] Ythan estuary, Aberdeenshire, Scotland. BM(NH) 1972.3.27.10.

—— [stomach] St. Andrews, Scotland. Collected by D. R. R. Burt. BM(NH) 1983.11.9.41.

—— [stomach] NW of Flannan Isles, Scotland (59°N, 08°W; depth 144 m; July, 1976). BM(NH) 1983.11.9.42.

—— [stomach] Whitby, Yorkshire, England (Jan., 1974). Collected by G. Boxshall. BM(NH) 1976.1.5.62–100.

—— [stomach] 'Dog Hole', off NE Scotland (57°N, 02°W; depth 75 m; May, 1983). BM(NH) 1983.6.21.4–13 and 1983.11.9.43.

Salmo trutta [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1983.11.9.44–63.

—— [?] Off Ringsend, Co. Dublin, Eire (July, 1978). Collected by E. Fahy. BM(NH) 1978.12.6.1–50 and 1979.3.1.11.

Scophthalmus rhombus [stomach] Aberdeen, Scotland (Oct., 1973). BM(NH) 1983.11.9.64–66.

Taurulus bubalis [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1983.11.9.67–68.
—— [stomach] Wembury, Plymouth, Devon, England (Oct., 1980). BM(NH) 1983.11.9.69.
Trachurus trachurus [?] Firth of Forth, Scotland (Aug., 1963). Collected by K. Mackenzie. BM(NH) 1983.11.9.70.
Trigloporus lastoviza [stomach] Plymouth, Devon, England (May, 1932). BM(NH) 1932.11.29.10 (Material of Baylis & Jones, 1933: 631).
Trisopterus luscus [stomach] Plymouth, Devon, England (Oct., 1980). BM(NH) 1983.11.9.71–72.
Trisopterus minutus [stomach] Off St. Kilda. Collected by Z. Kabata. BM(NH) 1963.6.21.39–43.
—— [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1983.11.9.73–82.
—— [stomach] Off North Rona, Scotland (59°N, 06°W; depth 84 m; May, 1984). BM(NH) 1984.7.20.66.
Zoarces viviparus [stomach] Firth of Forth, Scotland (July, 1963). Collected by K. MacKenzie, BM(NH) 1983.11.9.83.

(b) From elsewhere
None.

(ii) NE Atlantic records from the literature
Most of the 19th century records of *Distoma(-um)* and *Apoblema appendiculata* are listed here, as *H. communis* is the commonest species of the genus in the NE Atlantic region. Some of these records could, however, have been other species of the genus or even species of other genera.
(?) *Acipenser sturio** [stomach] Ireland. Bellingham (1844: 425; as *Distoma appendiculatum*).
(?) *Ammodytes tobianus* [stomach] Ireland. Bellingham (1844: 425; as *Distoma appendiculatum*).
Ammodytes tobianus [stomach] Varberg, Sweden (July, Aug.). Olsson (1868: 49, fig. 98; as *Distoma ocreatum* Molin: see Odhner, 1905: 352, footnote).
—— [oesophagus, stomach, intestine] St. Andrews, Scotland. Nicoll (1907: 71, 86).
—— [intestine] Northumberland coast, England (June). Lebour (1908: 56).
(?) *Anguilla anguilla* [stomach] St. Andrews, Scotland. Nicoll (1907: 72; as *H. appendiculatus)*.
Anguilla anguilla [stomach] St. Andrews, Scotland. Nicoll (1909: 6, 20).
—— [stomach] Bergen, Norway (Sept.). Olsson (1868: 46; as *Distoma appendiculatum*: see Odhner, 1905: 351).
Argentina sphyraena [?] British coast. Halliday, in Scott (1969: 882).
Aspitrigla cuculus [?] Plymouth, Devon, England. Nicoll (1914: 484).
Blennius pholis [stomach] Widemouth, Bude, Cornwall, England (July). Matthews (1982*b*: 152).
(?) *Brosme brosme* [?] Bergen, Norway (Aug.). Lönnberg (1890: 42; as *Distoma appendiculatum*).
Brosme brosme [stomach] Aberdeen, Scotland. Nicoll (1913: 190).
Capros aper [?] Plymouth, Devon, England. Nicoll (1914: 484).
Ciliata mustela [stomach] Kristineberg, Sweden (Aug., 1903). Dollfus (1960*b*: 705). Material of, but not mentioned by, Odhner (1905:351).
—— [stomach] Mumbles Head, Swansea, Wales. Srivastava (1966: 472).
—— [stomach, intestine] Widemouth, Bude, Cornwall, England (July, Aug.). Matthews (1982*b*: 161).
Conger conger [stomach] Plymouth, Devon, England. Baylis & Jones (1933: 631); Baylis (1939: 477).
—— [oesophagus, stomach, intestine] Roscoff, Finistère, France (June, 1937). Sproston (1939: 45, 50).
—— [stomach] St. Andrews, Scotland. Gordon, in Laverack & Blackler (1974: 35).
Coregonus lavaretus oxyrinchus [stomach, caeca] Varberg, Sweden (Aug.). Olsson (1868: 46; as *Distoma appendiculatum*: see Odhner, 1905: 351).
(?) *Dicentrarchus labrax* [?intestine] (Rennes), Brittany, France. Dujardin (1845: 420; as *Distoma* (*Apoblema*) *appendiculatum*).
Entelurus aequoreus [?] Plymouth, Devon, England. Nicoll (1914: 484); Dawes (1947: 279).
Eutrigla gurnardus [stomach] St. Andrews, Scotland. Nicoll (1909: 4, 20).
—— [?] Plymouth, Devon, England. Nicoll (1914: 484).
—— [intestine, stomach] North Sea, near Shetland Isles. Duniec (1980: 67; as *H. luehei*).
Gadus morhua [stomach] Varberg, Sweden; Ålesund & Bergen, Norway (June–Sept.). Olsson (1868, 46; as *Distoma appendiculatum*: see Odhner, 1905: 351).
(?) —— [?] Kristineberg, Sweden (Aug.). Lönnberg (1889: 58; as *Distomum appendiculatum*).
(?) —— [?] Bergen, Norway (July–Aug.). Lönnberg (1890: 40, 42; as *Distomum appendiculatum*).

*A very doubtful record. Other records from this host suggest that it might have been a lecithochiriine.

—— [stomach] Kristineberg, Sweden. Retzius (1909: 71); (July, 1898) Dollfus (1953: 78); (Aug., 1901) Dollfus (1953: 78); (Aug., 1903) Looss (1908: 106); Dollfus (1960*b*: 705). All material of, but not recorded by, Odhner (1905: 351).
—— [stomach] St. Andrews, Scotland. Nicoll (1909: 5, 20); Gordon, in Laverack & Blackler (1974: 35).
—— [stomach] Millport, Firth of Clyde, Scotland. Nicoll (1910: 350).
—— [stomach] Galway, Eire. Little (1929: 25).
—— [stomach] W of Scotland (July, 1954). Williams (1960: 708).
—— [stomach] West coast of Norway. Meskal (1967: 13).
—— [stomach] Scottish waters. Williams, McVicar & Ralph (1970: 48).
—— [stomach] Havstensfjord & Gulmarsfjord (Kristineberg), Sweden. Thulin (1971: 78). Öresund, Sweden. Thulin (1981: 22).
—— [stomach] Bergen fish market, Norway. Kryvi (1972: 243; 1973: 273).
—— [stomach] Kiel-Fjord, N Germany. Möller (1975*a*: 75; 1975*b*: 8).
—— [?] Western Kattegat to Bornholm in the Baltic. Køie (1981: 61).

Gaidropsarus mediterraneus [stomach] Widemouth, Bude, Cornwall, England (May). Matthews (1982*b*: 155).

(?) *Gasterosteus aculeatus* [stomach] Ostend, Belgium. van Beneden (1871: 40; as *Distoma appendiculata*).

(?) —— [?] Kristineberg, Sweden (July). Lönnberg (1889: 54; as *Distomum appendiculatum*).

—— [stomach] Kristineberg, Sweden (Aug., 1901). Dollfus (1960*b*: 705). Material of, but not mentioned by, Odhner (1905: 351).

Gobius niger [stomach] Kristineberg, Sweden (Aug., 1901). Dollfus (1960*b*: 705). Material of, but not mentioned by, Odhner (1905: 351).

Gobius paganellus [?] Plymouth, Devon, England. Nicoll (1914: 484).

Hippoglossoides platessoides [stomach] Bergen, Norway (July). Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner, 1905; 351).
—— [stomach] Millport, Firth of Clyde, Scotland. Nicoll (1910: 350, 357).

Hippoglossus hippoglossus [stomach] Bergen, Norway (Aug.). Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner, 1905: 351).
—— [stomach] St. Andrews, Scotland. Nicoll (1907: 72; as *Hemiurus appendiculatus*; 1909: 5, 20).
—— [?] Trondheim, Norway (Sept., 1905). Dollfus (1960*b*: 705).
—— [stomach] W of Scotland (July, 1954). Williams (1960: 708).

Hyperoplus lanceolatus [?] Plymouth, Devon, England. Nicoll (1914: 484).

Labrus bergylta [stomach] Millport, Firth of Clyde, Scotland. Nicoll (1910: 350, 356).

(?) *Lampetra fluviatilis* [intestine] Belgian coast. van Beneden (1871: 90; as *Distoma appendiculata*).

Lepadogaster lepadogaster [?] Plymouth, Devon, England. Nicoll (1914: 484).

(?) *Limanda limanda* [?] New Brighton, Cheshire, England. Johnstone (1906: [174] 318; as *Distomum appendiculatum*).
—— [stomach] Aberdeen, Scotland. Nicoll (1913:190).
—— [?] Western Kattegat and Øresund. Køie (1981: 61); [stomach] Øresund, Kattegat, off west Jutland (depth 10–32 m). Køie (1983: 204).

Liparis montagui [?] Northumberland, England. Crofton (1947: 62).

Lophius piscatorius [stomach] Plymouth, Devon, England. Nicoll (1914: 484); Baylis & Jones (1933: 631); Baylis (1939: 477); Dawes (1947: 279); Matthews (1982*b*: 151).
—— [?] NE Atlantic. Gaevskaja (1978*a*: 83; possibly not an original record).

(?) *Melanogrammus aeglefinus* [mouth, stomach, caeca, intestine] Belgian coast. van Beneden (1871: 57; as *Distoma appendiculata*).
—— [stomach] St. Andrews, Scotland. Nicoll (1907: 71, 86).

Merlangius merlangus [buccal cavity] Bergen, Norway (Aug.). Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner, 1905: 351).
—— [stomach] Kristineberg, Sweden (Aug., 1901). Dollfus (1960*b*: 705). Material of, but not recorded by, Odhner (1905: 351).
—— [stomach] Shoals, Irish Sea (March, 1906). Johnstone (1907: 280; as *Distomum appendiculatum*).
—— [stomach] Northumberland coast, England. Lebour (1908: 56).
—— [stomach] Plymouth, Devon, England. Nicoll (1914: 484); Baylis & Jones (1933: 631); Baylis (1939: 477); Dawes (1947: 279).
—— [stomach] Galway, Eire. Little (1929: 25).
—— [stomach] W of Scotland (July, 1954). Williams (1960: 708).
—— [stomach] Isle of Man, Irish Sea. Shotter (1969: 15; 1970: 36; 1972: 121; 1973*a*: 189; 1973*b*: 563; 1976: 103). Some of this material is probably *H. luehei*.

Micromesistius poutassou [stomach] Off Rockall (Nov., 1975). Mackenzie (1979: 10).
Molva molva [stomach] Bergen, Norway (Aug.). Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner, 1905: 351).
—— [stomach] Plymouth, Devon, England. Nicoll (1914: 484); Baylis & Jones (1933: 631); Baylis (1939: 477).
Myoxocephalus scorpius [stomach] Kristineberg, Sweden (Aug., 1901). Dollfus (1960*b*: 705). Material of, but not recorded by, Odhner (1905: 351).
—— [stomach] Bergen, Norway (Sept.). Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner, 1905: 351).
—— [intestine] Northumberland coast, England. Lebour (1908: 56); Crofton (1947: 62).
—— [stomach] Plymouth, Devon, England. Baylis & Jones (1933: 631); Baylis (1939: 477).
Pagellus bogaraveo [stomach] Aberdeen, Scotland. Nicoll (1913: 189).
—— [?] Plymouth, Devon, England. Nicoll (1912: 200; 1914: 484).
—— [stomach] Galway, Eire. Little (1929: 26).
Pholis gunnellus [intestine] St. Andrews, Scotland. Nicoll (1907: 71; as *Hemiurus appendiculatus*; 1909: 5, 20).
Platichthys flesus [stomach] Galway, Eire. Little (1929: 26).
(?) —— [?] Walney Channel, Barrow-in-Furness, Cumbria, England. Markowski (1966: 192; specimens in BM(NH) collection are *Brachyphallus crenatus*).
—— [stomach] Ythan estuary, Aberdeenshire; off Aberdeen; Loch Ewe, Scotland. MacKenzie & Gibson (1970: 4). Ythan estuary and Dee estuary, Aberdeenshire; sea off Aberdeen, Scotland. Gibson (1972: 6).
—— [?] Kiel-Fjord, N Germany. Möller (1974: 138; 1975*b*: 8).
(?) *Pleuronectes platessa* [?] New Brighton, Cheshire, England. Johnstone (1906: [174] 318; as *Distomum appendiculatum*).
—— [stomach] Galway, Eire. Little (1929: 26).
—— [stomach] Loch Ewe, NW Scotland. MacKenzie (1968: 15); MacKenzie & Gibson (1970: 4).
—— [?] (Fish farm) Ardtoe, Argyle, Scotland. DAFS (1972*a*: 42).
—— [?] (Fish farm) Hunterston, Ayrshire, Scotland. DAFS (1972*b*: 35).
—— [?] (Fish farm) Moidart, Inverness-shire, Scotland. MacKenzie *et al.* (1976: 4).
Pollachius pollachius [stomach] Bergen, Norway. (Aug.) Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner: 1905, 351). (July) Lönnberg (1890: 42; as *Distomum appendiculatum*).
—— [?] Kristineberg, Sweden. Juel (1889: 4; as *Apoblema appendiculatum*; see Odhner, 1905: 351). (July) Lönnberg (1889: 58; as *Distomum appendiculatum*).
—— [stomach] Millport, Firth of Clyde, Scotland. Nicoll (1910: 357).
—— [stomach] Aberdeen, Scotland. Nicoll (1913: 189).
—— [?] Plymouth, Devon, England. Nicoll (1914: 484).
—— [stomach] Galway, Eire. Little (1929: 25).
—— [stomach] W of Scotland (July, 1954). Williams (1960: 708).
—— [stomach] Isle of Man, Irish Sea. Cubbin (1969: 52).
Pollachius virens [stomach] Bergen, Norway. (Sept.) Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner, 1905: 351); (July) Lönnberg (1890: 42; as *Distomum appendiculatum*).
(?) —— [?] Kristineberg, Sweden (Aug.). Lönnberg (1889: 58; as *Distomum appendiculatum*).
—— [stomach] Millport, Firth of Clyde, Scotland. Nicoll (1910: 350, 356).
—— [stomach] Loch Craiglin, Argyll, Scotland. Raymont (1952: 111).
—— [stomach] Isle of Man, Irish Sea. Cubbin (1969: 51).
—— [stomach] Bergen Fish Market, Norway. Kryvi (1972: 243; 1973: 273).
Raniceps raninus [stomach] Kristineberg, Sweden (Jan., 1903). Dollfus (1960*b*: 705). Material of, but not mentioned by, Odhner (1905: 351).
Salmo salar [stomach] Varburg, Sweden (Aug.). Olsson (1968: 46; as *Distoma appendiculatum*; see Odhner, 1905: 351).
(?) —— [stomach] Bahusiae (? Bohuslän), Sweden (Aug.). Olsson (1876: 20; as *Distoma appendiculatum*).
(?) —— [stomach] Sundsvall, Sweden (July). Olsson (1893: 12; as *Distoma appendiculatum*).
—— [?] River Exe, Devon, England. Kennedy (1975: 66).
Salmo trutta [stomach] Bergen, Norway (Sept.). Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner, 1905: 351).
(?) —— [?] Kristineberg, Sweden (June). Lönnberg (1889: 58; as *Distomum appendiculatum*).
—— [stomach] Kristineberg, Sweden (Aug., 1902). Dollfus (1960*b*: 705). Material of, but not mentioned by, Odhner (1905: 351).
—— [?] t'Horntje, Texel, Netherlands. Willemse (1968: 84).

Scophthalmus rhombus [stomach] Bergen, Norway (Aug.). Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner, 1905: 351).
Sebastes marinus [stomach] East coast of Iceland (67°N, 12°W; depth 105 m; Aug., 1948). Rees (1953: 20).
Solea solea [stomach] Whitstable, Kent, England. El Maghraby & Perkins (1956: 486).
(?) *Taurulus bubalis* [?] Kristineberg, Sweden (July). Lönnberg (1889: 54; as *Distomum appendiculatum*).
—— [stomach] Kristineberg, Sweden (Sept., 1903). Dollfus (1960*b*: 705). Material of, but not mentioned by, Odhner (1905: 351).
—— [stomach] St. Andrews, Scotland. Nicoll (1907: 70; as *Hemiurus appendiculatus*; 1909: 4, 20).
—— [?] Plymouth, Devon, England. Nicoll (1914: 484).
—— [stomach] Roscoff, Finistère, France (June, 1937). Sproston (1939: 50).
—— [?] Northumberland coast, England. Crofton (1947: 62).
—— [stomach] Widemouth, Bude, Cornwall. Matthews (1982*b*: 158).
(?) *Torpedo marmorata* [stomach, intestine] Blankenberg, Belgium. van Beneden (1871: 16; as *Distoma appendiculata*).
Trachinus draco [stomach] Aberdeen, Scotland. Nicoll (1913: 189).
Trachurus trachurus [?] ?NE Atlantic. Gaevskaja & Kovaleva (1980*a*: 53; 1982: 61).
—— [?] English Channel. Gaevskaja & Kovaleva (1980*b*: 19).
(?) *Trigla lucerna* [stomach, intestine] Belgian coast. van Beneden (1871: 30; as *Distoma appendiculata*).
—— [stomach] Galway, Eire. Little (1929: 25).
—— [oesophagus] Roscoff, Finistère, France. Sproston (1939: 42).
Trigloporus lastoviza [stomach] Plymouth, Devon, England. Baylis & Jones (1933: 631); Baylis (1939: 477).
Trisopterus esmarkii [stomach] Faroes. Kabata, in Raitt (1968: 3–5).
Trisopterus luscus [?] Plymouth, Devon, England. Nicoll (1914: 484); Dawes (1947: 279).
—— [stomach] Galway, Eire. Little (1929: 25).
—— [gills] Roscoff, Finistère, France. Sproston (1939: 41, 50).
—— [stomach] St. Andrews, Scotland. Gordon, in Laverack & Blackler (1974: 35).
—— [?] Ría de Muros-Noya, NW Spain. Martinez Fernandez, in Cordero del Campillo *et al.* (1975: 84).
Trisopterus minutes [stomach] Bergen, Norway (Aug.). Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner, 1905: 351).
(?) —— [stomach] Bahusiae (? Bohuslän), Sweden (July, Aug.). Olsson (1876: 20; as *Distoma appendiculatum*; see Odhner, 1905: 351).
—— [stomach] Millport, Firth of Clyde, Scotland. Nicoll (1910: 350, 356).
—— [?] Plymouth, Devon, England. Nicoll (1914: 484).
Zeugopterus punctatus [?] Plymouth, Devon, England. Nicoll (1914: 484).

Aspects of biology. The full life-history of this species is not known, as information on the molluscan host and intra-molluscan stages is lacking. Presumably, the life-history follows a similar course to that believed to occur in other hemiurids, i.e. egg, miracidium/mother sporocyst, redia, cystophorus cercaria. Dollfus (1923) has suggested that *Cercaria calliostomae* Dollfus, 1923, from the prosobranch *Calliostoma zizyphinum* might be the 'larval' form of a species of *Hemiurus,* and, if so, it is clear that *H. communis* is by far the commonest species of *Hemiurus* in the region of Roscoff, Brittany, where Dollfus' material came from, and indeed around Plymouth, where this cercaria has been recorded by Matthews (1982*a,b*). Unfortunately, it appears that the molluscan host *Calliostoma zizyphinum* has a Lusitanean distribution which is much wider than that of *H. communis.* The metacercariae of this species have been recorded on several occasions in the north-east Atlantic region from copepods, such as *Acartia,* from chaetognaths, especially *Sagitta* spp. and ctenophores (see pp. 5) by authors such as Lebour (1923, 1935) and Meek (1928). It is not known whether chaetognaths and ctenophores acquire their infestations directly or by feeding upon infested copepods. Small fish and fish-fry must, however, acquire the parasite directly from copepods and other planktonic invertebrates, but the majority of the larger fish presumably become infested by feeding upon small plankton-feeders, such as sand-eels, and other smaller infested teleosts.

This parasite occurs in a wide variety of teleosts in British waters, but is especially common in gadoids. As discussed below, it is noticeably absent from pelagic, filter-feeding clupeids which harbour other species of the genus. As indicated by Gibson & Valtonen (1981) and Gibson (1982, 1983), *H. communis* has a distinctly boreal distribution (see below). Gibson (1972), studying this

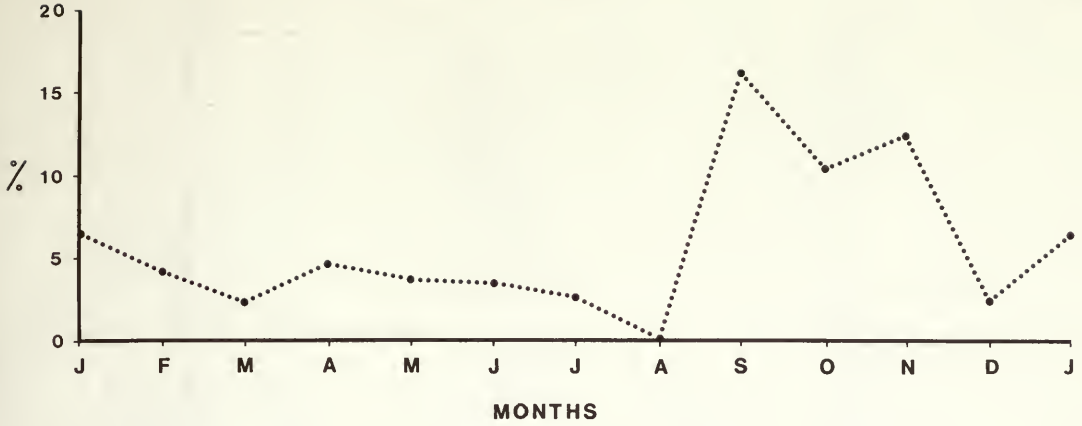


Fig. 2 *Hemiurus communis*. Seasonal prevalence in *Platichthys flesus* from the estuary of the River Ythan.

parasite in the flounder *Platichthys flesus* from two Scottish estuaries and from the sea nearby off Aberdeen, found it to be of little use as a biological tag.

Meskal (1967) deduced that the period of recruitment of young specimens of *H. communis* in the cod *Gadus morhua* off Norway commences in September, is at a maximum in November, and continues during the late autumn, winter and spring. He suggested that the old specimens die off between the summer and the following February. The life-span of this parasite in the cod appears, therefore, to be about eight months on average with a maximum of about 15 months. Gibson (1971), working with large numbers of flounders *Platichthys flesus* from the Ythan estuary, Aberdeenshire, found an autumnal peak in the prevalence of this parasite (Fig. 2). This peak is probably caused by flounders feeding upon small, infested saithe *Pollachius virens* and other small fishes which come inshore and often enter the estuaries at this time of the year, and by the addition of 0-group (recently metamorphosed) flounders to the population. These young fish presumably become infested by feeding directly upon planktonic invertebrates. Meskal (1967) noted a spring peak as well as an autumn peak in the prevalence of this parasite in cod. The absence of a spring peak in flounders can probably be explained by the fact that in spring, when normal feeding resumes after the winter reduction, many of the small teleosts which were eaten during the previous autumn are now too fast and too large to be eaten by flounders. In addition, many of the migratory forms, such as the saithe, will have moved back out to sea and away from the inshore and estuarine flounders.

Parasites with planktonic invertebrate hosts would be expected to infest most of the larger teleosts, firstly, when they are recently hatched and, secondly, when they are large enough to feed upon small, plankton-feeding fishes or smaller carnivorous forms. The results obtained by Gibson (1971) in flounders are presented in Fig. 3. These differ slightly from the expected results in relation to the younger fish, possibly because of the longevity of the parasite; those remaining from the 0-group infestation possibly obscuring a limited recruitment by 1-group fish.

As mentioned above, it is clear from the records that *H. communis* appears to have a relatively restricted boreal distribution. Most of the records are on the continental shelf between Trondheim in Norway and Brittany in France, and the majority of these occur within the latitudes of Great Britain, extending eastwards into the Baltic Sea. The extreme limits of the records in our region range from a single specimen off Iceland mentioned by Rees (1953) to its presence in the Ría de Noya, NW Spain, reported by Fernandez, in Cordero de Campillo *et al.* (1975). Outside our region, Polyanski (1955) indicated that it was rare in the Barents Sea, Pogorel'steva (1952) and Nikolaeva (1963) claim to have found it in the Black Sea, and Ronald (1960) lists it as occurring off the eastern coast of Canada. The isolation of the latter three records and the difficulties encountered in distinguishing this species from some other members of the family,

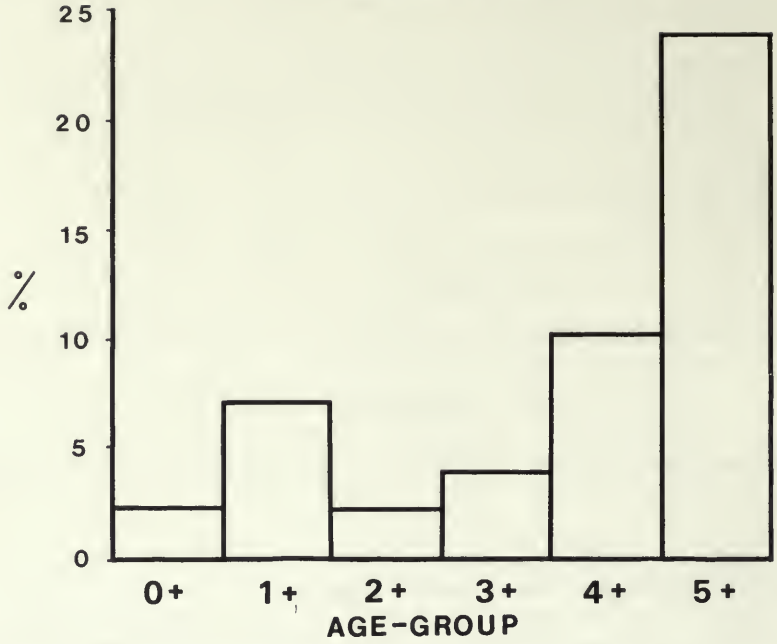


Fig. 3 *Hemiurus communis*. Prevalence in different age-groups of *Platichthys flesus* from the estuary of the River Ythan.

especially poorly preserved material, indicate, in our opinion, that the presence of this species in the Black Sea and on the western side of the Atlantic Ocean requires confirmation. Appy & Burt (1982) stated that *H. communis* may 'be absent from the western Atlantic' and called for confirmation of reports to the contrary.

Kryvi (1972, 1973) studied the ultrastructure of the tegument and suckers of this parasite.

PREVIOUS DESCRIPTIONS. Odhner (1905: 351; brief, no figure); Nicoll (1907: 86; no figure); Lebour (1908: 56); Looss (1908: 106; brief, no figure); Raymont (1952: 114; some morphometric details); Dollfus (1953: 73; 1960: 704; figures of types); Srivastava (1966: 472; brief); Reimer (1970: 78; brief).

DESCRIPTION (Figs 4 & 5). The body of this worm is elongate and fusiform, its length depending greatly upon the extent to which the *ecsoma* is extruded. The latter structure may be completely withdrawn or extended until it occupies more than one-third of the total length of the worm. It is noticeable in small specimens that a double invagination of this organ often occurs (see Fig. 4B). The body-surface is covered with annular *plications* (Fig. 4F) ventrally and laterally, although they become less distinct in the posterior region of the body-proper (soma). In the larger specimens the dorsal plications occur only at the anterior extremity, extending posteriorly to the level of the pharynx or the intestinal bifurcation; but in smaller specimens the plications may occur, often very distinctly, back to the level of the seminal vesicle (Figs 4 & 5). Plications do not occur on the ecsoma, although under certain conditions, and especially in frozen material, the presence of circular muscles in the body-wall can give rise to small annular ridges, both on the ecsoma and on the rest of the body (Fig. 4E). In specimens which have been frozen or allowed to relax in tap-water prior to fixation the annular plications may be lost. The *oral sucker* is ventrally subterminal and surmounted by a small pre-oral lobe. The *ventral sucker*, which is roughly one and a half to twice the size of the oral sucker (according to Raymont, 1952, this ratio increases slightly with the size of the worm), occurs well inside the anterior third of the soma. Measurements of this species are given in Table 2.

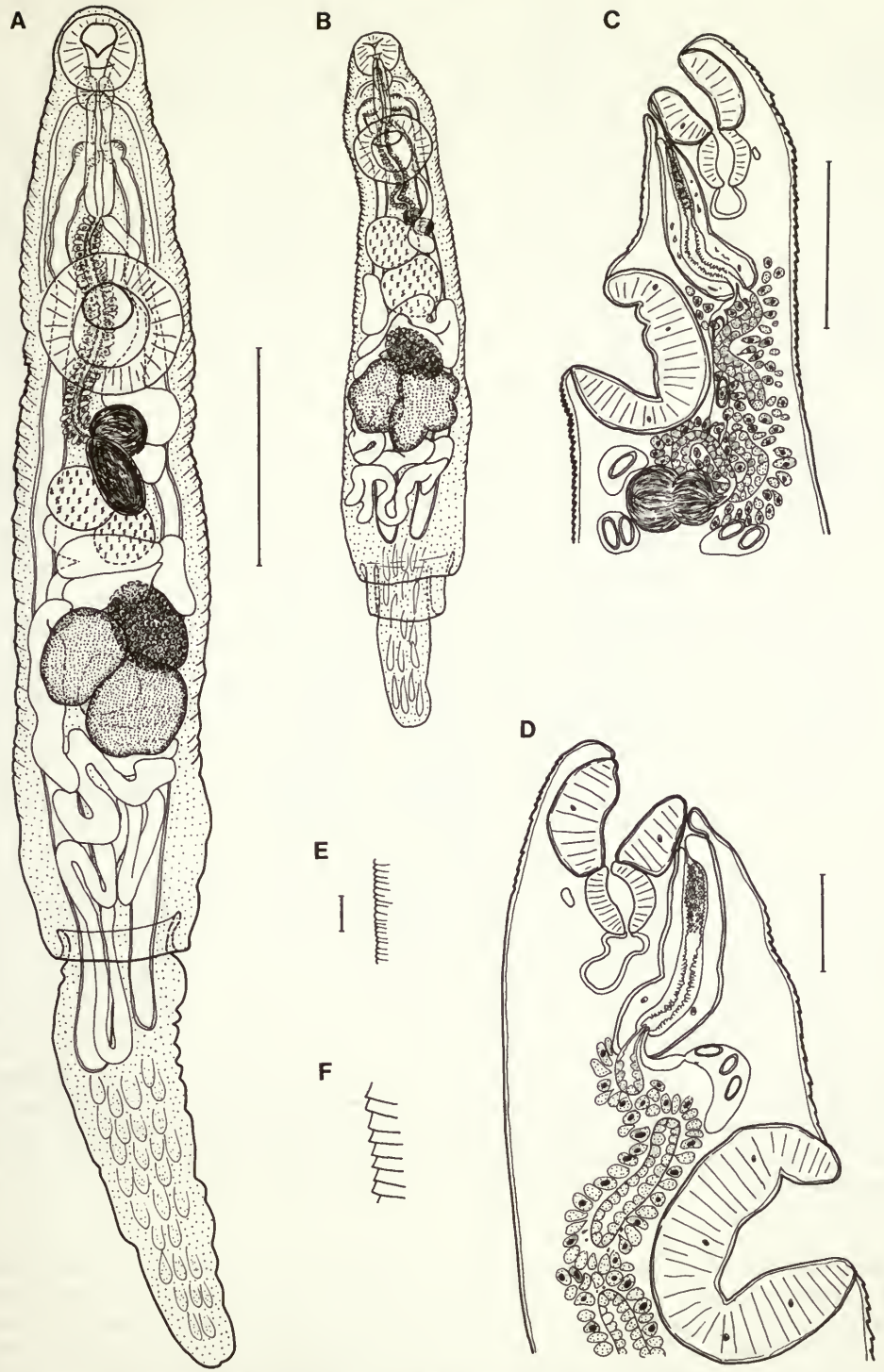


Fig. 4 *Hemiurus communis*. (A) Entire worm, ex *Merlangius merlangus*; (B) Entire worm, ex *Limanda limanda*; (C) Sagittal section of forebody, ex *Scophthalmus rhombus*; (D) Sagittal section of forebody, ex *Pollachius virens*; (E) Annulations on ecsomal surface of frozen specimen, ex *Platichthys flesus*; (F) Plications on surface of well-fixed specimen, ex *Limanda limanda*. Scale bars A,B 500 μm; C,D 100 μm; E,F 20 μm.

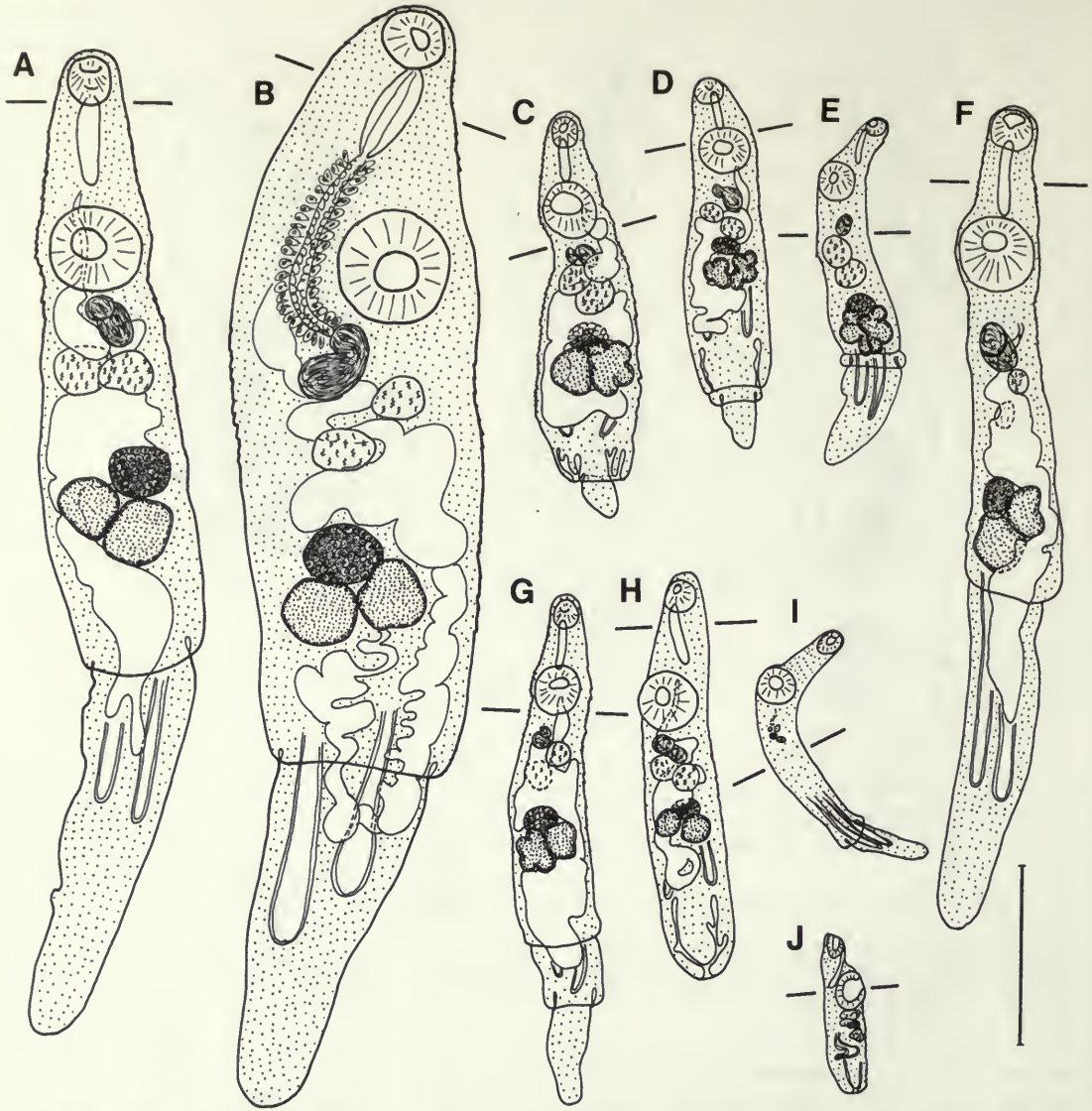


Fig. 5 *Hemiurus communis* showing variations in morphology, laterality and postero-dorsal limit of plications (marked with lateral bars). (A) ex *Gadus morhua*; (B) ex *Lophius piscatorius* (flattened); (C) ex *Salmo trutta*; (D) ex *Scophthalmus rhombus*; (E) ex *Pagellus bogareveo*; (F) ex *Conger conger*; (G) ex *Gadus morhua*; (H) ex *Cyclopterus lumpus*; (I) ex *Dicentrarchus labrax*; (J) ex *Trisopterus minutus*. Scale bar: 500 μm.

There is no prepharynx. The muscular *pharynx* gives rise posteriorly to a very short oesophagus which extends posteriorly or dorsally, depending upon the state of contraction, to its union with the gut-caeca. The latter pass laterally and immediately dilate to form oval 'Drüsenmagen', which possess an extremely deep, villous lining, before passing posteriorly. They pass back down the body dorso-laterally and end blindly near the posterior extremity of the soma, or, when the ecsoma is extruded, they may extend some distance, sometimes deeply, into it.

The excretory pore opens terminally on the ecsoma. It leads into a tubular, Y-shaped *excretory vesicle* which bifurcates at about the level of the testes. The stem, which may initially wind in

Table 2 Measurements of *Hemiurus communis*

Authority Host	Nicoll (1907) *Ammodytes tobianus*	Looss (1908) *Gadus morhua*	Dollfus (1960*b*) *Salmo trutta, Myoxocephalus scorpius, Raniceps raninus*	Present material Various hosts
Locality	St. Andrews, Scotland	West Sweden	Kristineberg, Sweden	Various localities
Length (mm)	1·5–2·5	2·0	1·8–3·53	0·45–4·0
Breadth (mm)	0·42–0·57	0·4–0·45	0·43–0·78	0·105–0·85
Ecsoma (mm)	<40 % body length	0·7	–	0–1·5
Forebody (mm)	–	–	–	0·11–0·6
Oral sucker (mm)	0·11–0·18 diam.	0·14 diam.	0·1–0·15 × 0·12–0·19	0·06–0·2 × 0·05–0·22
Ventral sucker (mm)	0·16–0·26 diam.	0·3 diam.	0·19–0·31 diam.	0·09–0·4 × 0·08–0·4
Sucker-ratio	1 : 1·5–2·0	–	–	1 : 1·57–2·3 (usually 1 : 1·7–1·9)
Testes (mm)	0·1–0·16 diam.	–	–	0·02–0·22 × 0·02–0·25
Ovary (mm)	0·11–0·16 × 0·09	–	–	0·01–0·2 × 0·02–0·22
Vitelline masses (mm)	–	–	–	absent–0·3 × 0·32
Eggs (μm)	22–31 × 9–13	19–21 × 10–12	21–24 × 9–12	22–29 × 9–15 (usually 24–28 × 10–12)

specimens with withdrawn ecsoma, passes forward medially and slightly dorsally. The arms extend into the forebody ventro-laterally and unite dorsally to the pharynx.

The two oval *testes* occur obliquely in the anterior half of the hind body, usually about halfway between the ovary and the ventral sucker. One of the testes is normally situated slightly more dorsally than the other, but this can be either testis and either of them can be the more anterior. It is noticeable that the testes especially are variable in size, but all of the gonads tend to be smaller in relation to body-size in the larger specimens. The seminal vesicle consists of two globular or oval, contiguous lobes which are situated between the testes and the ventral sucker and close to the latter. The proximal lobe of this organ is normally the larger, although both are very variable in size, and may be larger than the testes. The proximal lobe usually has a slightly thicker and more muscular wall, but the thickness of the wall of both the portions varies considerably, depending presumably upon the volume of spermatozoa contained. Distally, the seminal vesicle gives rise to a tubular pars prostatica, which is lined with anuclear projections (blebs) that almost fill the lumen, surrounded by a dense, but narrow, covering of gland-cells and possesses a wall containing distinct longitudinal muscle-bundles. The pars prostatica passes anteriorly, dorsal to the ventral sucker, following an initially sinuous but then more direct course, to join the base of the *sinus-sac*. As it passes through the wall of the sinus-sac, the male duct loses its lining and external gland-cells and assumes the form of an undifferentiated ejaculatory duct. This very short duct unites with the metraterm to form an hermaphroditic duct just within the base of the sinus-sac (Fig. 4C, D). The sinus-sac is a tubular structure with a thick, muscular wall. It initially runs antero-ventrally in the middle of the forebody from a level just anterior to the ventral sucker, and then curves to run anteriorly to join a very short genital atrium. The median genital pore occurs

close to the ventral margin of the oral sucker. The hermaphroditic duct, which extends throughout the length of the sinus-sac, has a wall which contains both longitudinal and circular muscles. The proximal (posterior) half of this duct is lined with what appears to be a villous coat, the 'villi' of which possess terminal and possibly detachable globules, somewhat similar to those described by Gibson (1976) in *Paradinurus manteri* Vigueras, 1958. The distal half of the duct is lined by a dense concentration of regular, papillate structures: this is, presumably, the region which is everted during copulation to form a temporary sinus-organ. There is no permanent sinus-organ.

The subglobular *ovary* is situated close to the middle of the body, its position varying to some extent with the degree of contraction and/or the extent to which the ecsoma is extruded. It is normally separated from the testes by loops of the uterus. Details of the ovarian complex, which occurs postero-dorsally to the ovary, are difficult to make out, as it is very compact. The oviduct appears, however, to leave the ovary postero-dorsally, and, as it receives both the duct from Juel's organ and the common vitelline duct, it passes into a compact Mehlis' gland. The arrangement is, therefore, almost certainly very similar to that described below in detail for *H. levinseni* (see p. 30). Juel's organ is well developed, consisting of an oval 'inner vesicle', which contains active and disintegrating spermatozoa and an eosinophilic substance, and a surrounding amorphous mass, which contains a few, large, nucleate cells resembling amoebocytes. In some specimens the 'inner vesicle' of Juel's organ can be swollen with spermatozoa, giving the false impression that a small seminal receptacle is present (e.g. Dollfus, 1960*b*, fig. 1). In live specimens the 'inner vesicle' is very evident as a distinct, oval structure containing active spermatozoa. Egg-formation occurs in the proximal few narrow loops of the uterus, a region which we refer to as the uterine oötype (see Gibson & Bray, 1979). The next part of the uterus is wider and filled with spermatozoa, thus forming a distinct uterine seminal receptacle. The uterus then loops posteriorly, following a convoluted course, usually extending into the proximal region of the ecsoma when the latter is extruded. It then loops forward, filling much of the hindbody dorsally and also ventrally between the ovary and the testes and at the level of the seminal vesicle, before leading more directly forward dorsally to the ventral sucker. The uterus can pass the vitellarium on either the right or the left side of the body, but the dextral form seems to be slightly more common. In some specimens the distal extremity of the uterus, prior to its entry into the base of the sinus-sac, is constricted (Fig. 4C,D), forming a small vesicle which resembles that occurring in the genus *Erilepturus* Woolcock, 1935 (= *Uterovesiculurus* Skrjabin & Guschanskaja, 1954). Within the sinus-sac the short metraterm unites with the ejaculatory duct to form the hermaphroditic duct. The uterus is normally filled with a great number of small, operculate eggs which lack spines or filaments. The *vitellarium* is composed of two large, symmetrical and oval or lobed masses, which occur immediately posterior to the ovary. In the larger specimens the vitelline masses are unlobed, but in the smaller worms the degree of lobation varies (Fig. 5). When present, the lobes occur as three on one mass and four on the other. It is interesting that the mass with three lobes appears to be associated with the side of the body on which the uterus passes the vitellarium, so that there are distinct sinistral and dextral forms of this species. The vitelline ducts unite to form a common duct before the latter joins the oviduct.

Discussion. During the course of our study of this worm, it became clear that well-fixed specimens could usually be split into two morphological groups:

A. Specimens which: (1) were 0·5 to 4·0 mm, but rarely less than 1 mm, in length; (2) were less distinctly plicated, the plications reaching dorsally no further back than the level of the intestinal bifurcation; (3) possessed unlobed vitelline masses; and (4) tended to possess only single invaginations of the ecsoma (see Fig. 5).

B. Specimens which: (1) were 0·5 to 2·5 mm, but rarely greater than 2 mm, in length; (2) were distinctly plicated, the plications reaching back dorsally to a level between the middle of the ventral sucker and the testes; (3) possessed lobed vitelline masses; and (4) tended to possess double invaginations of the ecsoma (see Fig. 5).

There appear to be no host-differences, as we have specimens of both forms from cod and other gadoids, although the 'B'-form appears to be more prevalent in sand-eels and flatfishes. It is rather interesting that our specimens from the type-host and locality are the 'B'-form, while

Dollfus' (1960*b*) figures of the syntypes are clearly form 'A'. It seems most likely that form 'B' is merely a younger condition of form 'A'. This is suggested by some of the features which distinguish them, i.e. the posterior limit of the dorsal plications and the degree of lobation of the vitelline masses, which vary in the same manner, although to a lesser extent, in other species of the genus. It might seem, however, that there is more to distinguish these two forms than separates *H. appendiculatus* and *H. luehei*; but in the latter case there are distinct host-differences, and in the case of *H. communis* there are specimens which could be considered as intermediate between the two forms. In our view, therefore, there is not sufficient evidence to justify splitting the traditional concept of *H. communis* into two. It may be worthwhile to emphasize that some of the distinguishing features mentioned above are visible only in well-fixed material (our specimens were fixed without pressure in G.A.A. or Berland's fluid) which have been removed from freshly killed hosts.

One intriguing feature of this species is that, except for one immature specimen from *Sprattus sprattus* recorded by Reimer (1970) in the Baltic Sea, *H. communis* does not appear to have been found in clupeids. Considering that *H. appendiculatus* occurs only in certain clupeids and that *H. luehei* is common in certain clupeids, this is surprising, especially as *H. communis* is so common in a wide range of marine teleosts, its metacercaria occurs in planktonic invertebrates (assuming the determinations of these larval forms in the literature is correct), and because clupeids are plankton-feeders. This phenomenon suggests that some sort of physiological or immunological host-specificity is involved, for, unless small plankton-feeding fish, such as sand-eels, are obligatory intermediate hosts, and this does seem unlikely, it is difficult to envisage how any ecological host-specificity might apply.

Hemiurus levinseni Odhner, 1905

(?) *Fasciola serrulata* Müller, 1780.
(?) *Hemiurus serrulatus* (Müller) Dollfus, 1968.
(?) *Fasciola scabrum* Müller, 1784.
(?) *Distoma scabrum* (Müller) Zeder, 1803.
(?) *Distoma* (*Echinostoma*) *scabrum* (Müller) of Rudolphi (1819) in part.
(?) *Apoblema scabrum* (Müller) Juel, 1889.
Distoma appendiculatum (Rudolphi) of Olsson (1868) in part and Levinsen (1881).
Distomum ocreatum Molin of Linton (1900, 1901) in part.
*Hemiurus lintoni** Pratt, in Linton, 1901.
Hemiurus (*Metahemiurus*) *levinseni* (Odhner) Skrjabin & Guschanskaja, 1954.
Metahemiurus levinseni (Odhner) Brinkmann, 1975.
Hemiurus odhneri Yamaguti, 1934.

TYPE-HOST AND LOCALITY. *Boreogadus saida,* Franz-Joseph's Fjord, East Greenland.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Arctogadus sp. (? *pearyi*) [stomach] NE Greenland (Aug., 1931). Collected from preserved fish by J. Thulin. BM(NH) 1983.11.15.1–2.
Boreogadus saida [stomach] Claveringfjord, NE Greenland (Aug., 1931). Collected from preserved fish by J. Thulin. BM(NH) 1983.11.15.3–5.
Gadus morhua [stomach] Tromsø, Norway (June, 1980). BM(NH) 1980.6.20.42–43.
Hippoglossus hippoglossus [stomach] Ingolfshofdi, South Iceland (Oct., 1966). Collected by B. Manger. BM(NH) 1983.11.15.6–7.
Merlangius merlangus [stomach] Off NE Scotland (60°N, 01°E; depth 116 m; July, 1976). BM(NH) 1983.11.15.8–9.
Merluccius merluccius [stomach] Thistle Field, northern North Sea (61°N, 01½°E; depth 160 m; May, 1983). BM(NH) 1983.11.15.10.

*Although this name, which was proposed by Pratt, in Linton (1901) for Linton's material referred to as *'Distomum ocreatum* Molin', is older than *H. levinseni,* it has remained unused. For the sake of stability (Article 23b of the ICZN 1985), and because Linton's material was probably a mixture of *H. levinseni* and *Brachyphallus crenatus* (Rud., 1802), we have refrained from using it.

Micromesistius poutassou [stomach] Thistle Platform, North Sea (61°N, 01°E; depth 168 m; May, 1984). BM(NH) 1984.7.20.62.

Salmo salar [?] River North Esk, Angus, Scotland. Collected by J. W. Smith. BM(NH) 1967.10.2.20–22.

—— [intestine] River Lee, Eire (March, 1967). Collected by M. Kane. BM(NH) 1968.4.16.2.

Trisopterus esmarkii [stomach] Locality unknown, but probably off the Scottish coast. Collected by Z. Kabata. BM(NH) 1983.11.15.11–13.

Trisopterus minutus [stomach] North Sea, E of the Shetlands (60°N, 00½°E; June, 1975). Collected by G. Kruse. BM(NH) 1981.4.21.1–2.

(b) From elsewhere

Alosa pseudoharengus [stomach] Passamaquoddy Bay, New Brunswick, Canada (Aug., 1982). BM(NH) 1982.9.28.62–71.

Boreogadus saida [stomach] Grand Bank, W of Newfoundland (47°N, 52°W; depth 172 m; July, 1975); Grand Bank, NW of Newfoundland (49°N, 51°W; depth 188 m; July, 1975); Hamilton Inlet Bank, Labrador, Canada (54°N, 54°W; depth 188 and 192 m; July, 1975). BM(NH) 1977.2.17.1–12 (Material of Bray, 1979: 421).

Gadus morhua [stomach] Funk Island Bank, NW of Newfoundland (51°N, 52°W; depth 226 m; July, 1975); Banquereau, W of Nova Scotia, Canada (44°N, 57°W; depth 76 m; July, 1975); Banquereau, N of Nova Scotia, Canada (45°N, 57°W; July, 1975). BM(NH) 1977.2.17.13–20 (Material of Bray, 1979: 421).

Hemitripterus americanus [stomach] Sable Island Bank, off Nova Scotia, Canada (43°N, 61°W; depth 72 m; July, 1975). BM(NH) 1977.2.17.21–24 (Material of Bray, 1979: 421).

—— [stomach] Passamaquoddy Bay, New Brunswick, Canada (Aug., 1982). BM(NH) 1982.9.28.95–96.

Hippoglossus hippoglossus [stomach] Hamilton Inlet Bank, off Labrador, Canada (54°N, 55°W; depth 176 m; July, 1975). BM(NH) 1977.2.17.25 (Material of Bray, 1979: 421).

Myoxocephalus octodecemspinosus [stomach] Sable Island Bank (43°N, 61°W; depth 72 m; July, 1975). BM(NH) 1977.2.17.26 (Material of Bray, 1979: 421).

Phycis chesteri [?] Scotian Shelf, Canada (Jan., 1979). Collected by J. S. Scott. BM(NH) 1983.1.21.3–6.

Reinhardtius hippoglossoides [stomach] Hamilton Inlet Bank, W of Labrador, Canada (54°N, 54°W; depth 192 m; July, 1975). BM(NH) 1977.2.17.27 (Material of Bray, 1979: 421).

Urophycis chuss [stomach] Passamaquoddy Bay, New Brunswick, Canada (Aug., 1982). BM(NH) 1982.9.28.60–61.

(ii) NE Atlantic records from the literature

Boreogadus saida [stomach] Franz-Joseph's Fjord, East Greenland. Odhner (1905: 349).

Eutrigla gurnardus [stomach, intestine] North Sea, near Shetland Isles. Duniec (1980: 67).

Gadus morhua [stomach] W of Shetland Isles (Sept., 1954). Williams (1960: 708).

Micromesistius poutassou [intestine] Bergen, Norway (Aug.). Olsson (1868: 46; as *Distoma appendiculatum*; see Odhner (1905: 348).

—— [?] Off Spitsbergen (77°N, 12°E) and/or Faroe Isles (62°N, 06°W). Szuks, Lorenz & Steding (1978: 144).

—— [?] ?North Sea, Celtic Sea, SW Irish Sea ?or Bay of Biscay. Gaevskaja (1978*b*: 4).

Phycis blennoides [mouth] Skagen, Denmark. Odhner (1905: 349, footnote).

(?) *Pollachius pollachius** [intestine] Ireland. Bellingham (1844: 427; as *Distoma scabrum*).

(?) ——* [intestine] Ostende, Belgium (June). van Beneden (1871: 61; as *Distoma* (*Echinostoma*) *scabra*).

(?) *Pollachius virens* [stomach] Loch Craiglin, Argyllshire, Scotland. Raymont (1952: 116; as *Hemiurus communis*).

Salmo salar [?] British Isles. Pippy (1980: 78).

(?) *Trisopterus esmarkii* [stomach] Faeroe Isles. Kabata, in Raitt (1968: 3, 5).

(?) *Trisopterus luscus* (as *Gadi barbati*)** [stomach] Denmark (Nov.). Müller (1780: 3; as *Fasciola serrulata*; 1784: 31; as *F. scabrum*).

*These records are very questionable as they lack descriptions and because Rudolphi (1819) appears to have possibly confused *Fasciola serrulata* (=*F. scabrum* of Müller) with the acanthocolpid genus *Stephanostomum* Looss, 1899. According to Looss (1899) and Odhner (1905: 65, footnote) this led to the inclusion of this species with the echinostomes.

**Earlier workers have listed the host of Müller's record as being *Gadus morhua*, but according to our information *Gadus barbatus* is a synonym of *Trisopterus luscus*. This species is not, however, common in Danish waters, although its close relative *T. esmarkii* is, and the latter species is known to harbour *H. levinseni*. *Fasciola serrulata* and *F. scabrum* have been listed as possible synonyms of both *Hemiurus* sp. by Looss (1899) and *H. communis* by Odhner (1905) and as a definite record of *H. communis* by Dollfus (1968). However, the sucker-ratio in Müller's (1780) figures and the identity of the host which we favour suggests to us that, although *H. communis* and *Brachyphallus crenatus* cannot be ruled out, this species is most likely a synonym of *H. levinseni*.

Aspects of biology. Little is known about the biology of this species, but it is assumed that it has a similar life-history to *H. communis*. Scott (1969) presumed the second intermediate hosts off the eastern Canadian coast to be *Acartia* and *Sagitta*, but so far only *Sagitta elegans* has actually been incriminated, both in the Gulf of St. Lawrence by Weinstein (1966, 1967, 1974) and in the White Sea by Kulachkova (1972*a*,*b*). Nevertheless, it is worth noting that Walter *et al.* (1979) have recorded *Hemiurus* sp. (presumably *H. levinseni*) from the White Sea in *Temora longicornis*, *Acartia longiremis* and *Pseudocalanus elongatus*.

Although *H. levinseni* appears essentially to be a parasite of gadoids and to a lesser extent salmonids, it is clear that it must initially be acquired by plankton-feeding fishes (including juvenile predatory fishes) before being passed on to the larger predatory fishes. As in the case of *H. communis* (see above), this parasite does not appear to occur in clupeids in our region. The nature of this apparent host-specificity may, however, be different to that exhibited by *H. communis*, as *H. levinseni* is known to occur in the NW Atlantic in *Clupea* (Cooper, 1915; Miller, 1941; Gaevskaja & Umnova, 1977) and *Alosa* (Gaevskaja & Umnova, 1977; see also p. 26), and in the North Pacific in *Clupea* (Skrjabina, 1963; Arthur & Arai, 1980).

The paucity of our knowledge concerning this species prohibited Margolis (1963) from any definite conclusion on its value as a biological indicator of salmon in the northern North Pacific, and Scott (1969) showed that it was not suitable as an indicator for *Argentina silas* on the eastern coast of Canada. In his study of *H. levinseni*, Scott (1969) noted that 100 % prevalence occurred in young specimens of *A. silas* with an intensity of up to 200 per fish, falling to a low prevalence of about 15 % in mature fish with an intensity close to zero. Off the eastern Siberian coast Mamaev & Oshmarin (1963) reported that the prevalence in cod reached 92 % with an average intensity of 58, while it was totally absent in herring. They also stated that their results indicated that the parasite was acquired by fish in the sublittoral zone. In freshwater they found a prevalence of 4–7 % in *Oncorhynchus nerka*, and deduced that the range of this parasite in different species of salmon extended from the spawning ground in freshwater to the deep water of the northern Pacific Ocean. More recently, Appy & Burt (1982) found a prevalence of 89·7 % (up to 100 % in some regions) in cod in Canadian Atlantic waters.

H. levinseni appears essentially to be an arctic-boreal species (see Bray, 1979; Gibson & Valtonen, 1981; Gibson, 1982, 1983), probably having a circum-polar distribution which extends southerly into the northern North Atlantic and the northern North Pacific Oceans, especially, and to a greater extent, on the cooler western sides of these oceans. It occurs, therefore, only in the northern part of the area covered by this series, extending only as far south as the British Isles. As pointed out by Bray (1979) the record of this parasite from the Indian Ocean by Parukhin (1976*a*) would appear to be very doubtful. It is worth noting that *H. levinseni* occupies a similar niche in arctic-boreal waters as does the hemiurid *Elytrophalloides oatesi* (Leiper & Atkinson, 1914) in antarctic-antiboreal waters.

Previous descriptions. Odhner (1905: 349); Looss (1908: 106); Cooper (1915: 188; encapsulated specimens); Manter (1926: 92); Yamaguti (1934: 432; as *H. odhneri*); Lloyd (1938: 115); Linton (1940: 123); Margolis (1956: 207; abnormal specimen); Zhukov (1960: 33); Hill (1974: 544); Grabda (1978: 21). (Many of these descriptions are brief.)

Description (Fig. 6). This small, spindle-shaped worm is relatively constant in shape, its *ecsoma* usually being either withdrawn or protruding only a short distance and rarely exceeding one quarter of the total body-length (Fig. 6). The body-surface, except for the ecsoma, is covered ventrally and laterally with annular *plications*, although these tend to fade out towards the posterior extremity. Dorsally the plications extend only as far back as the region between the ventral sucker and the ovary, but usually reach to the level of the testes. The *oral sucker* is ventrally subterminal, being surmounted by a small pre-oral lobe. The forebody is relatively long, usually being about one quarter of the total length of the soma, although it is sometimes less in contracted specimens. The *ventral sucker*, which is situated well inside the anterior half of the body, is similar in size to the oral sucker, the sucker-ratio (normally 1 : 0·9–1·1) not varying with body-size. Measurements of this species are given in Table 3.

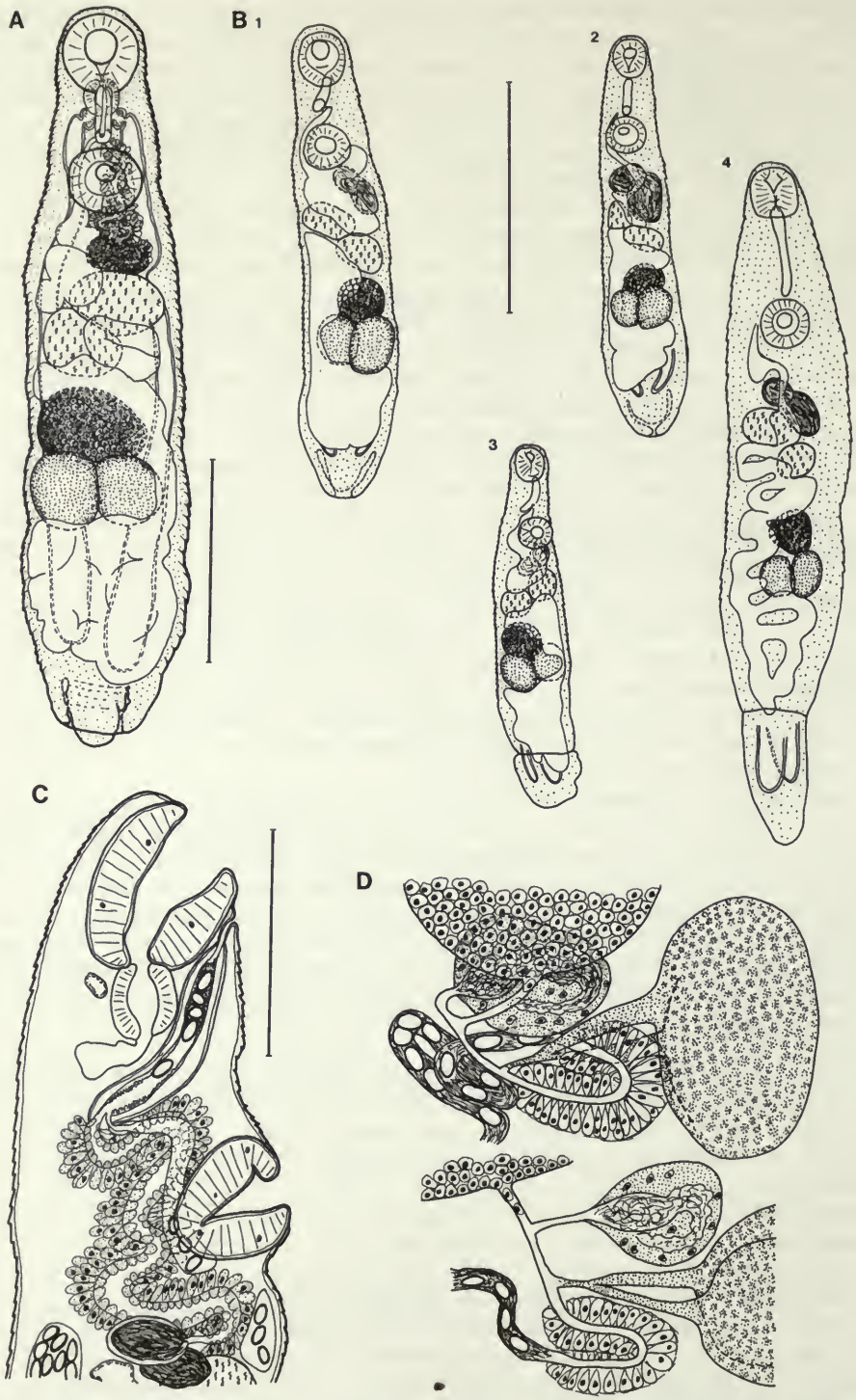


Fig. 6 *Hemiurus levinseni*. (A) Entire worm, ex *Merlangius merlangus*; (B) Entire worms, ex: (1) *Gadus morhua*, (2) *Trisopterus esmarkii*, (3) *Hemitripterus americanus*, (4) *Salmo salar* (flattened); (C) Sagittal section of forebody, ex *Boreogadus saida*; (D) Ovarian complex, ex *Boreogadus saida*: above, lateral view, below, exploded diagram. Scale bars: A 500 μm; B 1 mm; C 200 μm.

Table 3 Measurements of *Hemiurus levinseni*

Authority Host	Odhner (1905) *Boreogadus saida*	Manter (1926) *Gadus morhua, Urophycis chuss*	Zhukov (1960) *Theragra chalcogramma, Onchorhynchus gorbuscha*	Present material Various hosts
Locality	Franz-Joseph's Fjord, East Greenland	Maine, USA	Sea of Japan, Sea of Okhotsk	Various North Atlantic localities
Length (mm)	1–1·6	0·99–1·68	1·3–4·16	0·79–2·9
Breadth (mm)	1/3 length	0·37–0·47	–	0·17–0·55
Ecsoma (mm)	withdrawn	withdrawn	–	0–0·6
Forebody (mm)	–	–	–	0·19–0·63
Oral sucker (mm)	0·14–0·2 diam.	0·14–0·18 diam.	–	0·1–0·23 × 0·09–0·23
Ventral sucker (mm)	0·11–0·17 diam.	0·14–0·19 diam.	–	0·08–0·22 × 0·08–0·23
Sucker-ratio	Oral > ventral	*c.* 1 : 1	–	1 : 0·84–1·1
Testes (mm)	–	–	–	0·07–0·21 × 0·06–0·25
Ovary (mm)	–	–	–	0·08–0·23 × 0·07–0·26
Vitelline masses (mm)	–	–	–	0·1–0·25 × 0·07–0·23
Eggs (μm)	26–28 × 12–13	23–26 × 10–13	25–29 × 12–13	20–27 × 10–15 (usually 23–26 × 10–13

There is no prepharynx, but the muscular, oval *pharynx* opens into a short, tegumental oesophagus which divides just posterior to the pharynx, giving rise to two dilate, lateral caeca which almost immediately open into the 'Drüsenmagen'. These, in turn, open into the main part of the gut-caeca, which possess a glandular lining and extend back in the dorso-lateral fields. The rather wide caeca pass backwards, often sinuously, and terminate blindly either close to the base of the invaginated ecsoma or, when the latter is evaginated, often deep within it.

The excretory pore opens terminally on the ecsoma. It leads into a tubular, Y-shaped *excretory vesicle* which passes forward dorsally to the ovarian complex and bifurcates at a level between the anterior testis and the seminal vesicle. The arms pass forward laterally in the forebody and unite dorsally to the pharynx.

The two relatively large, globular or oval *testes* occur close together ventrally and obliquely, the dextral one being the more anterior, between the ovary and the ventral sucker and usually just anterior to the middle of the body. In relation to the size of the body, the testes are larger than in other species of the genus (in our specimens from salmon the testes are smaller than those in specimens recovered from other hosts; Fig. 6B4). The seminal vesicle consists of two oval lobes: these vary greatly in size, although the posterior (proximal) thin-walled lobe is usually the larger, sometimes exceeding the testes in size. The anterior (distal) lobe has a thicker wall, although it is not quite as thick as that of *H. appendiculatus* and *H. luehei*, and communicates with the pars prostatica via a short, aglandular duct (Fig. 6C). The tubular pars prostatica is much shorter than occurs in the latter two species and similar to that of *H. communis*. It winds between the seminal vesicle and the base of the sinus-sac, especially in the region immediately anterior to the seminal vesicle, passing dorsally to the ventral sucker. It is surrounded by a relatively dense concentration of external gland-cells, which may be up to two cells in thickness (cf. *H. appendiculatus*), and to be lined by a layer of blebs (anuclear projections). At about the level of the anterior

margin of the ventral sucker the pars prostatica passes, with the distal extremity of the uterus, through the wall of the proximal extremity of the *sinus-sac*. The ejaculatory duct is extremely short, as, once within the sinus-sac, the male and female ducts unite to form the hermaphroditic duct. The sinus-sac is tubular or slightly claviform, being slightly wider proximally. It lies medially, passing antero-ventrally and then curving to run anteriorly ventral to the pharynx before uniting with an extremely small genital atrium. This, in turn, opens to the exterior through the genital pore, which is situated mid-ventrally, close to the ventral margin of the oral sucker. As in the other species of the genus, the hermaphroditic duct appears to be divided into regions. The distal half is lined with a regular arrangement of small, tegumental knobs. This region is linked by a short, smooth region to the proximal half of the duct, which is lined by an irregular villous layer that appears to 'secrete' the extremities of the small 'villi' into the lumen (cf. the blebs lining the pars prostatica and also the ejaculatory vesicle of some lecithochiriines).

The large *ovary* is usually globular, but it is occasionally oval. It occurs close to the middle of the hindbody (excluding the ecsoma), being either contiguous with the posterior testis or, more often, separated from it by a small portion of the uterine coils. The remainder of the ovarian complex, present posterior or postero-dorsal to the ovary, is easier to decipher than in the other species of the genus. The oviduct passes posteriorly or postero-dorsally from the ovary and unites with the duct from Juel's organ, before curving ventrally to pass into Mehlis' gland. Immediately prior to its entry into this organ it receives the common vitelline duct. The part of the ovo-vitelline canal within Mehlis' gland can be referred to as the oötype, as the eggs do appear to be formed there. Having passed anteriorly or antero-dorsally it leaves Mehlis' gland and widens to become the *uterus* (Fig. 6D). The initial coils of the uterus dorsal and immediately posterior to Mehlis' gland contain spermatozoa in addition to eggs and, therefore, form a uterine seminal receptacle. Juel's organ (see Gibson & Bray, 1979) is large and surrounded by a distinct membrane. It occurs dorsally or antero-dorsally to the vitellarium and is often visible in whole-mounts (Fig. 6D). The 'inner vesicle' is somewhat tubular, being wide distally, but then narrowing proximally. It is irregularly convoluted within the organ and contains a loose concentration of what are presumably active spermatozoa which have recently passed through the oötype. The outer region of Juel's organ contains the usual amorphous material and quite a large number of cells which may be amoebocytes. The uterus winds posteriorly dorsal to the vitellarium until close to the base of the ecsoma, where it reflexes and loops forward ventrally, passing the vitellarium and the ovary on either the right or the left side of the body. Although forms with the uterus passing to the right of the vitellarium and the ovary (i.e. dextral forms) appear to be more common, the distribution of these forms in many cases does not appear to be random. All of our material from salmonids and the majority of our material from *Merlangius, Hemitripterus* and *Boreogadus* from the Hamilton Inlet Bank, Labrador, are sinistral, whereas the majority of our specimens from *Gadus, Trisopterus* and *Boreogadus* from off the Grand Banks, Newfoundland, are dextral. The uterus only occasionally extends into the ecsoma. Anterior to the ovary the uterus is quite wide. It passes forward to the right or the left side of the posterior testis in dextral and sinistral forms, respectively, although often partly overlapping it both ventrally and dorsally. It may or may not loop between the ovary and the posterior testis. After passing the anterior testis dorsally it usually loops ventrally or ventro-sinistrally to the pars prostatica, before narrowing and passing forward dorsally to the ventral sucker. At the level of the anterior margin of this sucker it enters the base of the sinus-sac, although often looping slightly into the forebody before doing so. The uterus contains numerous small, oval, operculate eggs which lack spines or filaments. The *vitellarium* is composed of two symmetrical, or occasionally slightly oblique, oval to globular masses which are present ventrally immediately posterior to the ovary. Even in the smallest specimens, there is little or no sign of any lobation on these masses.

Discussion. *Hemiurus levinseni* can be readily distinguished from the other species of the genus by sucker-ratio. Otherwise, it is morphologically somewhat similar to *H. communis*, although tending to have larger gonads and a less frequently evaginated ecsoma. It is also worth noting that even the smallest of our specimens were mature and gravid: this was not the case with the other species.

Skrjabin & Guschanskaja (1954) erected the subgenus *Metahemiurus* for *H. levinseni,* which they proposed as the type-species, and *H. odhneri* Yamaguti, 1934, because: (1) the oral sucker is larger than the ventral sucker; (2) the plications extend almost to the posterior end of the soma; and (3) the ecsoma is short. With a few exceptions (e.g. Slusarski, 1958; Brinkmann, 1975), the majority of workers have not accepted *Metahemiurus* as a valid taxon. Despite the fact that Brinkmann (1975) has used this name at the generic level, we cannot agree that there is any value in retaining this taxon, especially as we consider only some of the distinguishing criteria to be of value, and these only at the specific level. With regard to *H. odhneri,* we agree with Zhukov (1960) that this species falls within the morphometric range of *H. levinseni* and must, therefore, in the absence of other evidence, be considered a synonym.

Hemiurus luehei Odhner, 1905*

(?) 'vermiculos' of Leeuwenhoek (1697).
(?) *Fasciola halecis* Gmelin, 1790 (Leeuwenhoek's 'vermiculos' named).
(?) *Distoma halecis* (Gmelin) Zeder, 1803.
(?) *Hemiurus halecis* (Gmelin) Dollfus, 1956.
Fasciola ocreata Rudolphi, 1802, *nec* Goeze, 1782 *(nom. nov. pro Fasciola halecis* Gmelin*).*
Distoma ocreatum (Rudolphi) Rudolphi, 1809.
Distoma (*Apoblema*) *ocreatum* (Rudolphi) Dujardin, 1845.
Apoblema ocreatum (Rudolphi) Juel, 1889.
Pronopyge ocreata (Rudolphi) Looss, 1899.
Hemiurus ocreatus (Rudolphi) Odhner, 1911.
Distoma appendiculatum (Rudolphi, 1802) of Olsson (1868) (in part).
(?) *Distoma* (*Apoblema*) *appendiculatum* (Rudolphi) of Dujardin (1845) (in part).
Hemiurus appendiculatus (Rudolphi) of Rioja (1923), (?) Dollfus (1929) and Patzelt (1930).
Distoma ventricosum Rudolphi, 1819 of Wagener (1860) (in part).
Hemiurus stossichi (Monticelli, 1891) of Lühe (1901*a*).
'*Hemiurus stossichi* Lühe, 1901' of Odening (1978).
Hemiurus rugosus Looss, 1907.
Hemiurus (*Neohemiurus*) *raabei* Slusarski, 1958.
Parahemiurus merus (Linton, 1910) of Rokicki (1973) and Gaevskaja (1977).

Type-host and locality. *Clupea harengus,* Ålesund, Norway. In the absence of a previously designated type-host and locality, we have used the first records given by Olsson (1868) on whose material Odhner (1905) erected this species.

Records

(i) Material studied
(a) From the NE Atlantic
Brama brama [stomach] Buckie, Banff, Scotland (Oct., 1973). BM (NH) 1983.11.21.1.
Clupea harengus [stomach] Off NE Scotland (58°N, 02°W; depth 80 m; Dec., 1979). BM(NH) 1983.11.21.2.
—— [?] Moray Firth (winter 1972–73). Collected by K. MacKenzie, BM(NH) 1983.11.21.3.
—— [stomach] Turbot Bank, off NE Scotland (57°N, 01°W; depth 67 m; June, 1982). BM(NH) 1983.11.21.4.
Eutrigla gurnardus [?] Scotland, Collected by K. MacKenzie. BM(NH) 1983.11.21.5.
Merlangius merlangus [intestine] Burnham-on-Crouch, Essex, England. BM(NH) 1962.11.1.1.
—— [?] Port Erin, Isle of Man, Collected by R. A. Shotter. BM(NH) 1969.1.9.1. (Possibly part of material called *H. communis* by Shotter, 1969:15; 1970:36; 1972:121; 1973*a*: 189; 1973*b*: 563; 1976: 103).
Platichthys flesus [stomach] Off Aberdeen, Scotland. BM(NH) 1972.3.27.11. (Material of Gibson, 1973: 463).
—— [stomach] Ythan estuary, Aberdeenshire, Scotland (July, 1968). BM(NH) 1983.11.21.6.
Salmo salar [stomach] South of Dogger Bank, North Sea (55°N, 03°E). Collected by K. MacKenzie. BM(NH) 1983.11.21.7–40.

*Originally referred to as *H. lühei,* but the spelling of this name has since been amended in accordance with the International Code of Zoological Nomenclature.

Salmo trutta [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1983.11.21.41–43.
Sardina pilchardus [stomach] Bay of Biscay (47°N, 02°W; Mar., 1980). BM(NH) 1983.11.21.44–45.
Scomber scombrus [stomach] St. Andrews, Scotland (July, 1949). Collected by D. R. R. Burt, BM(NH) 1983.12.14.11.
Sprattus sprattus [stomach] Estuary of Riven Ythan, Aberdeenshire, Scotland. BM(NH) 1983.11.21.46.
—— [stomach] Off Macduff, Banff, Scotland (58°N, 02°W; depth 100 m; May, 1984) BM(NH) 1984.7.20.61.

(ii) From elsewhere
Clupea harengus membras [?] Baltic Sea (Apr., 1976). BM(NH) 1981.12.3.9. (Material of Gaevskaja, 1977:11: as *Parahemiurus merus*).

(b) NE Atlantic records from the literature
Capros aper [stomach] Plymouth, Devon, England. Nicoll (1914: 485; as *Hemiurus ocreatus*).
(?) *Clupea harengus* [stomach] Netherlands (March). Leeuwenhoek (1697: 47; as 'vermiculos'; later named *Fasciola halecis* by Gmelin, 1790, and renamed *Fasciola ocreata* by Rudolphi, 1802).
—— [stomach] Bløden Ground, North Sea (1953). Hansen (1955: 62).
—— [stomach] Ålesund and Bergen, Norway (July, Aug.). Olsson (1868: 46; as *Distoma appendiculatum*; renamed *H. lühei* by Odhner, 1905: 351).
—— [intestine] Belgian coast. van Beneden (1871: 66; as *Distoma appendiculata*).
—— [?] SE of West-Hinder (Dec., 1933); WNW of West-Hinder, 30 miles (48 km) from Ostende (Nov., 1933); 12 miles (19 km) W of West-Hinder (Dec., 1933). Markowski (1938: 6; as *H. ocreatus*).
—— [stomach and caecum] St. Andrews, Scotland. Nicoll (1907: 72, 87).
—— [stomach] Millport, Firth of Clyde, Scotland. Nicoll (1910: 350, 357).
—— [?] Den Helder, Netherlands. Willemse (1968: 84; as *H. ocreatus*).
—— [?] Northern North Sea. Reimer & Jessen (1972: 65).
—— [?] Irish Sea (Sept.). Markowski (1938: 6; as *H. ocreatus*).
—— [?] Near Gravelines, Pas de Calais, France (Jan., 1934); between Gravelines and Calais, France, outside territorial waters (Dec., 1933 & Jan., 1934); Calais, France (Jan., 1933). Markowski (1938: 6; as *H. ocreatus*).
Eutrigla gurnardus [stomach] St. Andrews, Scotland. Nicoll (1909: 4, 21).
Gadus morhua [?] Western Kattegat to Bornholm in the Baltic. Køie (1981: 61; as *H. ocreatus*).
Merlangius merlangus [stomach] Plymouth, Devon, England. Nicoll (1914: 485; as *H. ocreatus*).
Merluccius merluccius [stomach] Aberdeen, Scotland (Sept., 1908). Nicoll (1913: 189; as *H. ocreatus*).
—— [stomach] Galway, Eire. Little (1929: 26; as *H. ocreatus*).
Platichthys flesus [stomach] Off Aberdeen, Scotland. Gibson (1973: 463; as *H. ocreatus*).
—— [?] Kiel Fjord region, North Germany. Möller (1975*b*: 8; as *H. ocreatus*).
Pollachius pollachius [stomach] Plymouth, Devon, England. Nicoll (1914: 485; as *H. ocreatus*).
(?) *Salmo salar* [gut] River Rhine at Basle, Switzerland.*
—— [stomach] River Tweed, Great Britain. Tosh (1905: 116; as *Distoma ocreatum*).
Salmo trutta [?] River Tweed, Great Britain. Tosh (1905: 116; as *D. ocreatum*).
Sardina pilchardus [stomach] Plymouth, Devon, England. Nicoll (1914: 485; as *H. ocreatus*).
—— [oesophagus] Marin, Pontevedra, Spain. Rioja (1923: 89; as *H. appendiculatus*). See also: Lopez-Neyra (1941: 332; 1947: 57).
—— [?] Muros-Noya, NW Spain. Martinez-Fernandez, in Cordero del Campillo *et al.* (1975: 84; as *H. ocreatus*).
(?) *Scomber scombrus* [?intestine] Brittany (Rennes), France, Dujardin (1845: 420; as *Distoma (Apoblema) appendiculatum*).
—— [stomach] Plymouth, Devon, England. Nicoll (1914: 485; as *H. ocreatus*).
—— [stomach] St. Andrews, Scotland. Gordon, in Laverack & Blackler (1974: 35; as *Pronopyge ocreata*).

**Hemiurus luehei* may have been recorded by Zschokke (1896: 776) and Hausmann (1897: 22) under the names *Distomum ocreatum* and/or *Distomum appendiculatum*; but Heitz (1918: 344) has listed these records as *Brachyphallus crenatus* (Rudolphi, 1802). As Heitz had fresh material and access to the literature of Odhner, Looss and Lühe, we have accepted his opinion. It is possible, however, that Zschokke (1890: 764; 1891: 697; 1896: 773) and Hausmann (1897: 4) recorded *H. luehei* under the name '*Distomum reflexum* Creplin', for, although Zschokke's (1891) measurements are larger than those normally recorded for this species, his figure is somewhat similar if he confused the pars prostatica with the testes and the withdrawn ecsoma with the excretory vesicle. Earlier, van Beneden (1871) recorded '*D. reflexum*' from salmon, but his figure of this species from *Cyclopterus lumpus* appears to be rather similar to *Derogenes varicus* (Müller). *Distoma reflexum* Creplin is in fact a species of the opecoelid genus *Podocotyle* Dujardin. '*D. reflexum* Creplin' of Zschokke was referred to as '*Distomum* sp. nov.' by Lühe (1909).

Sprattus sprattus [stomach] Varberg, Sweden (July, Aug.). Olsson (1868: 46; as *Distoma appendiculatum*; renamed *H. lühei* by Odhner, 1905: 351).
—— [stomach] Bergen, Norway (July, Aug.). Olsson (1868: 46; as *Distoma appendiculatum*; renamed *H. lühei* by Odhner, 1905: 351).
(?) —— [caeca and intestine] Belgian coast. van Beneden (1871: 67; as *Distoma appendiculata*).
—— [stomach, caeca and intestines] St. Andrews, Scotland. Nicoll (1909: 4, 21).
—— [?] North Sea (over wide area). Reimer (1978: 149).
Trachurus trachurus [stomach] Plymouth, Devon, England. Nicoll (1914: 485; as *H. ocreatus*).
—— [?] English Channel. Gaevskaja & Kovaleva (1980*b*: 19).
—— [?] ?NE Atlantic. Gaevskaja & Kovaleva (1980*a*: 53; 1982: 61).
Trigloporus lastoviza [mouth] Roscoff, Brittany, France (June, 1937). Sproston (1939: 42, 55; as *H. ocreatus*).

Aspects of biology. Although Möbius, in Willemoes-Suhm (1871: 383) appears to have recorded ecsomate trematodes which he refers to as '*Distoma ocreatum* Rud. der Häringe' from copepods in the Bay of Kiel, there seems to be no more certain record of the larval stages of this parasite. It is assumed, however, that it has a similar life-history to the other species of the genus, and that the metacercariae occur in planktonic invertebrates, such as copepods and chaetognaths. Hansen (1955) noted that 95 % of the diet of herring was crustaceans and most of these were calanoids. Thus the clupeid hosts presumably acquire the parasites directly; but it seems likely that the non-clupeids acquire the parasite, at least in part, by feeding upon clupeids or other plankton-feeders. We know this to be the case in flounders from the Ythan estuary, Aberdeenshire, which became infested by feeding upon sprats, and Tosh (1905) noted that this parasite occurred in salmon and sea-trout, especially after they had been feeding upon herring. The apparent absence of this species from shad is difficult to explain, unless some sort of ecological or physiological specificity associated with their spawning migration into freshwater is involved, or unless immunological specificity occurs.

Little is known about the seasonal dynamics of this species, except that Hansen (1955) indicated that in North Sea herring prevalence is very low in winter, it increases in spring, is very high (about 70 %) in summer and falls again during the autumn.

The distribution of *H. luehei* appears to mimic that of one of its major definitive hosts, *Sprattus sprattus*. The records extend between the latitudes of 35° and 65°N on the Atlantic coast of Europe and extend easterly into the Baltic, Mediterranean and Black Seas. There appears to be no definite record west of the continental shelf off Britain, thus, as mentioned by Gibson & Valtonen (1981) and Gibson (1982, 1983), this species of parasite has a Lusitanean distribution. As mentioned above, it may extend its range into freshwater in salmonids, and it has been recorded in carnivorous freshwater fishes, e.g. Reimer (1970) found it in *Esox* in the Baltic Sea and Borovitzkaya (1952) and Kulakovskaya & Koval (1973) have recorded it in *Perca* in the lower Danube.

Little else is known about *H. luehei*. It is worth noting that Gibson (1973) observed the presence of 'excretory corpuscles' in the excretory vesicle under the TEM.

Previous descriptions. Odhner (1905: 352); Nicoll (1907: 85); Looss (1908: 105; as *H. lühei* and *H. rugosus*); Rioja (1923: 89; as *H. appendiculatus*; see also Lopez-Neyra, 1941: 332; 1947: 57); Patzelt (1930: 6; as *H. appendiculatus*); Timon-David (1937: 17; as *H. rugosus*); Slusarski (1958: 384; as *H. lühei* and *H. raabei*); Reimer (1970: 76).

Description (Fig. 7). The body of this species is cylindrical, the posterior half usually being broader than the anterior half (Fig. 7). Even when the *ecsoma*, which can reach up to one third of the total body-length, is completely withdrawn, the body is still very elongate and cylindrical. The body-surface, except for the ecsoma, is covered ventrally and laterally with distinct annular *plications*. These tend to become less distinct towards the posterior end of the soma. Dorsally the plications tend to reach posteriorly as far as the level of the seminal vesicle or the testes. The *oral sucker* is ventrally subterminal and surmounted by a small pre-oral lobe. The *ventral sucker*, which is often directed antero-ventrally, is situated close to the oral sucker. It is about one and a

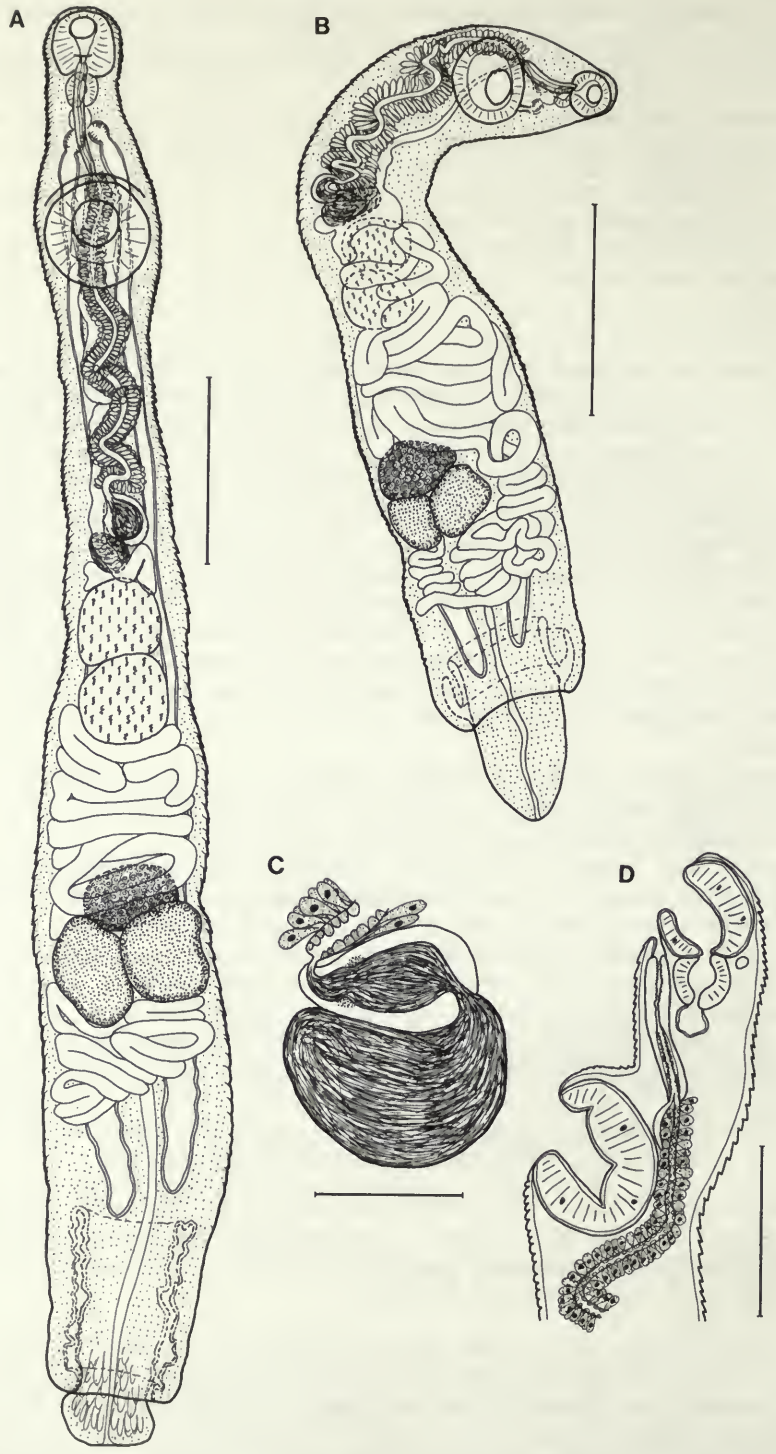


Fig. 7 *Hemiurus luehei*. (A) Entire worm, ex *Salmo trutta*; (B) Flattened worm, ex *Platichthys flesus*; (C) Seminal vesicle; (D) Sagittal section of forebody, ex *Salmo trutta*. Scale bars: A 200 μm; B 500 μm; C,D 100 μm.

Table 4 Measurements of *Hemiurus luehei*

Authority	Nicoll (1907)	Slusarski (1958)	Reimer (1970)	Present material
Name used	*H. lühei*	*H. raabei*	*H. luehei*	*H. luehei*
Host	*Clupea harengus*	*Salmo salar*	*Clupea harengus, Esox lucius*	Various hosts
Locality	St. Andrews, Scotland	Baltic Sea	Baltic Sea	Various localities
Length (mm)	2·7–4·14	1·8–2·62	0·77–2·38	0·8–2·9
Breadth (mm)	0·35–0·4	0·27–0·34	0·17–0·4	0·13–0·5
Ecsoma (mm)	1/4–1/3 soma	<1/3 soma	–	0–0·65
Ecsoma/body-length (%)	20–25	(<25)	–	0–31
Forebody (mm)	0·33–0·4*	–	–	0·08–0·27
Oral sucker (mm)	0·11–0·13 diam.	0·09–0·1 diam.	0·38–0·11 × 0·66–0·11	0·06–0·13 × 0·06–0·12
Ventral sucker (mm)	0·18–0·24 diam.	0·15–0·16 × 0·19–0·2	0·1–0·2 × 0·08–0·18	0·09–0·19 × 0·1–0·22
Sucker-ratio	1 : 1·5–2	1 : 1·6–1·9	–	1 : 1·43–2 (usually 1 : 1·5 –1·8)
Seminal vesicle to ventral sucker/body-length (%)	>25	–	–	13–28
Testes (mm)	0·14–0·16 diam.	–	0·03–0·15 × 0·05–0·19	0·06–0·13 × 0·05–0·18
Ovary (mm)	0·13–0·18 × 0·11–0·12	–	0·04–0·16 diam.	0·04–0·13 × 0·06–0·23
Vitelline masses (mm)	similar to ovary	–	0·08–0·21 diam.	0·05–0·19 × 0·05–0·2
Eggs (μm)	22–28 × 11–12	17–27 × 8–11	19–25 × 9–13	21–25 × 8–13

*Measurement from centre of sucker.

half to twice the size of the oral sucker, the ratio usually being about 1 : 1·5–1·8. The measurements of this species are given in Table 4.

There is no prepharynx, but the muscular, oval *pharynx* gives rise to a short, oval oesophagus with a tegumental lining, which extends posteriorly and, in turn, give rise laterally to the gut-caeca. The latter bear 'Drüsenmagen' in the 'shoulder'-region. The caeca then pass posteriorly, following a direct course in the dorso-lateral fields, and end blindly close to the posterior end of the body, normally within the ecsoma. The caeca usually extend only into the proximal half of the ecsoma when it is protruded, although normally further than the uterus; but occasionally they may almost reach the posterior end. When the ecsoma is withdrawn, the caeca may not enter it at all (Fig. 7A).

The excretory pore is terminal on the ecsoma. The *excretory vesicle* is Y-shaped, the narrow stem passing forward medially in the hindbody dorsal to the vitellarium and dividing in the ventral field at the level of the seminal vesicle. The two arms pass forward laterally into the forebody and unite dorsally to the pharynx.

The two oval *testes* occur in tandem or slightly obliquely just anterior to the middle of the hindbody (excluding the ecsoma) and slightly posterior to a point half-way between the ventral sucker and the ovary; but these arrangements are somewhat variable, depending upon the state of contraction. The seminal vesicle, which occurs immediately anterior to the testes, consists

of two contiguous, oval lobes, the anterior of which possesses a thick, muscular wall and is occasionally without spermatozoa. This lobe, which is usually the smaller of the two, is usually tear-shaped, often with its tapering distal region constricted slightly by a sphincter muscle (Fig. 7C). In some cases, this constriction can give the impression that the seminal vesicle is trilobed. The tapering region of the anterior lobe leads directly into a very long, tubular pars prostatica. This duct, which is surrounded by a relatively dense, but single, layer of oval gland-cells and lined by a layer of anuclear blebs, passes forward in the ventral field following a convoluted or sinuous path, depending upon the state of contraction. After passing the ventral sucker dorsally it unites with the metraterm just inside the base of the *sinus-sac* at about the level of the anterior margin of this sucker (Fig. 7D). The ejaculatory duct, i.e. the region of the male duct within the sinus-sac, is very short. The sinus-sac is usually cylindrical, but sometimes the proximal third is slightly pinched off into a broad, oval region. It possesses a thick, muscular wall and extends anteriorly to unite with a very small genital atrium, which opens mid-ventrally through the genital pore medially and close to the ventral margin of the oral sucker. Within the sinus-sac the hermaphroditic duct can be seen to be divided into two distinct regions which are united by a short, undifferentiated region of the duct. The nature of the two regions of this duct is not absolutely clear in our sectioned specimen, which is small; but they appear to be similar to other species of the genus in that the proximal region appears to possess an irregular, villous lining and the distal region possesses a regular, papillate (knobbed), tegumental lining.

The transversely oval *ovary* is usually present about half-way between the testes and the posterior end of the soma and is separated from the testes by a large proportion of the uterine coils. Although its position is variable, depending upon the degree of contraction, unlike *H. appendiculatus,* it does not appear to enter the ecsoma. The remainder of the ovarian complex is compact and difficult to decipher, but a distinct Juel's organ with an oval 'inner vesicle' is visible. After receiving the duct from Juel's organ and the common vitelline duct proximally, the oviduct then passes through Mehlis' gland. The initial coils of the *uterus,* which lie dorsally to the vitellarium, contain spermatozoa, and thus form a uterine seminal receptacle. The uterus continues posteriorly following a convoluted course usually into the proximal region of the ecsoma, although on rare occasions it can extend close to the posterior extremity and in some cases, when the ecsoma is withdrawn, it does not penetrate the ecsoma at all. The uterus then reflexes anteriorly, passing dorsally to the ovarian complex and following a convoluted course. The greatest region of uterine coils is between the ovary and the posterior testis, where they completely fill the entire width of the worm. The uterus passes the testes, seminal vesicle and pars prostatica dorsally, being either coiled, sinuous or running forward relatively directly. In this region it becomes narrower and then passes forward to enter the base of the sinus-sac. A short distance prior to its entry into this organ, there are indications in some specimens of a constriction caused by a sphincter muscle. The uterus is filled with numerous small, operculate eggs which lack spines or filaments. The *vitellarium* is composed of two entire or slightly lobed masses which occur symmetrically and ventrally immediately posterior to the ovary. The lobes, which normally occur as three on one mass and four on the other, are more often seen in small specimens.

Discussion. It seems likely that this species was first recorded by Leeuwenhoek (1697) in herring. Unfortunately, his description is not really adequate to indicate either the species or the genus, for, although it does seem likely that it was *H. luehei,* related forms, such as *Brachyphallus crenatus* (Rudolphi, 1802), have occasionally been recorded from herring in European waters. Leeuwenhoek's material was later named *Fasciola halecis* by Gmelin (1790), and this was again renamed *Fasciola ocreata* and redescribed from his own material by Rudolphi (1802). Unfortunately, the latter is a junior homonym of *F. ocreata* Goeze, 1782, which is now the type-species of *Ityogonimus* Lühe, 1899. This homonymity was probably overlooked because *F. ocreata* of Goeze (1782) and *F. ocreata* of Rudolphi (1802) were quickly transferred to *Monostoma* and *Distoma* by Zeder (1800) and (1803), respectively. Although Odhner's (1911) examination of Rudolphi's material has shown conclusively that it is a *Hemiurus,* there was considerable confusion concerning this name during much of the latter half of the 19th century. As we have explained in our publication on the Fellodistomidae (Bray & Gibson, 1980), the

appellation *Distoma (-um) ocreata (-um)* was used by several authors for the species which we now refer to as *Pronoprymna ventricosa* (Rudolphi, 1819). In addition, specimens of the present species were often referred to as *Distoma appendiculatum*. The first available name which we can be absolutely certain pertains to the species of *Hemiurus* which occurs commonly in the stomachs of herring, sprats and pilchards is *H. luehei* Odhner, 1905, and this is the name which we are accepting in this work. The majority of recent workers have used the name *H. ocreatus* (Rudolphi, 1802), since Odhner (1911) considered it a senior synonym of *H. luehei*; but the homonymity described above definitely precludes its usage (ICZN 1985, Article 57b). Dollfus (1956, 1968) has resurrected Gmelin's name and referred to this species as *Hemiurus halecis*; but, as mentioned above, we cannot be absolutely certain about the identity of Leeuwenhoek's material. Although the term 'nomen oblitum' has now been deleted from the ICZN, we feel that, as the name had remained unused since before 1830, except for two references to it as a junior synonym, it would, in any case, be unwise to resurrect it now.

Since Odhner's (1905) work, in which he listed *Hemiurus stossichi* (Monticelli, 1891) of Lühe (1901) as a possible synonym of *H. luehei,* Looss (1907, 1908) erected the name *H. rugosus* for Lühe's material. In agreement with Dawes (1947), Slusarski (1958), Reimer (1970) and others, we can see no reason for retaining *H. rugosus* as a distinct species. In addition, Slusarski (1958) erected *H. raabei* as a distinct form which he based on seven specimens from a single salmon in the Baltic Sea. He distinguished it from *H. luehei,* which he found in the same host and locality, essentially on the basis of a tripartite seminal vesicle (he actually refers to this as a seminal vesicle plus two accessory seminal vesicles) and the presence of narrow, cuticular folds covering the soma and the ecsoma. The latter can easily be dismissed, as these 'folds' are not plications, which never occur on the ecsoma, but small, annular ridges associated with the presence of circular muscle-bands in poorly preserved material. These ridges, which differ markedly from plications (i.e. posteriorly oriented tegumental thickenings), can occur not only in this worm, but also in other species of the genus (Fig. 4E), especially in material which has been slowly fixed in hypotonic solutions or frozen prior to fixation: the loss of plications, caused by the expansion of the body, also occurs under these conditions. The apparent presence of a three-lobed seminal vesicle* can possibly also be discounted, as it is clear in some of our whole-mounts that the thin-walled region of the seminal vesicle is often elongate and there are indications that it may possess a medial sphincter. Certainly, sphincters are the usual mechanism for constricting the contents of thin-walled seminal vesicles in other hemiurids. There also appears to be a sphincter present surrounding the region of the distal lobe of the seminal vesicle where it begins to taper towards the pars prostatica (Fig. 7C). Until the presence of a trilocular seminal vesicle as a constant feature is proved beyond doubt, we cannot accept *H. raabei* as a distinct species. It goes without saying, therefore, that we do not accept Slusarski's subgenus *Neohemiurus,* which he erected for *H. raabei* because of the presence of 'cuticular annuli' on the ecsoma. It is worth noting that Rokicki (1973, 1975) claimed to have found two specimens and Gaevskaja (1977) a single specimen of *H. raabei* in *Clupea harengus* in the Baltic Sea.

The major taxonomic problem with *H. luehei* is, however, to prove conclusively that it is distinct from *H. appendiculatus*. Certainly, one can easily find differences between the two species, such as: (1) *H. luehei* tends to be much smaller; (2) the plications on the dorsal surface normally extend much further posteriorly in *H. luehei*; (3) when extruded the ecsoma in *H. luehei* occupies a smaller proportion of the total body-length, i.e. normally less than one third, as opposed to up to a half; (4) the uterus at the level of the pars prostatica in *H. luehei* tends to be narrow and relatively straight or sinuous, whereas in *H. appendiculatus* it is usually swollen with eggs and often loops ventrally to the pars prostatica; (5) the sucker-ratio is slightly smaller in *H. luehei*; (6) the forebody is slightly shorter in *H. luehei*; (7) the distance between the seminal vesicle and the ventral sucker is slightly greater in *H. luehei* in relation to the size of the soma; and (8) there is a host-difference, *H. luehei* occurring in *Clupea harengus, Sprattus sprattus, Sardina*

*Despite Slusarski's comments, we still refer to the entire structure as being the seminal vesicle, as this organ is by definition merely a dilation of the vas deferens which acts as a seminal store.

pilchardus and their predators, and *H. appendiculatus* occurring in *Alosa* spp. It could be argued that *H. appendiculatus* is merely an older form of *H. luehei,* as many of the differences between the two species are consistent with variations and allometry observed in different sizes of specimens in other species of the genus. Similarly, the fact that *Alosa* spp. tend to live longer than herring, sprats and pilchards may suggest why larger forms occur only in these species, although evidence of the longevity of worms may negate this, and the absence of the larger form in non-clupeid hosts might be because shads do not tend to reach the sea until they are the size of mature sprats, because shads grow to a greater size than the other three clupeids, and because they are not as abundant as the latter. Nevertheless, we have examined very small specimens of *H. appendiculatus* from *Alosa fallax* which have features, such as the size of the ecsoma, sucker-ratio and dorsal limit of the plications, which are consistent with those of larger specimens from the same host. Until, therefore, there is experimental evidence to the contrary, we accept *H. luehei* as a distinct species.

Genus ***PARAHEMIURUS*** Vaz & Pereira, 1930

Although *Parahemiurus merus* (Linton, 1910) is claimed to occur in the south-eastern Baltic Sea (Rokicki, 1973; Gaevskaja, 1977), such records are very questionable. If indeed this species does occur on the eastern side of the Atlantic, its distribution is likely to be restricted to the south of European waters, since most of the records in the literature are from tropical American localities. Fischthal & Thomas (1971, 1972*a*) have recorded it as occurring off west Africa. Nevertheless, it is worth noting that in the Pacific it is claimed to extend northwards into more temperate waters and has been recorded in the Pacific herring by Arthur & Arai (1980) off British Columbia.

Rokicki (1973) claimed to have found a single specimen of this species in the Baltic herring. He stated that it had an oval seminal vesicle and that the pars prostatica arising from it formed a 'slight expansion' which was 'not like (as) another seminal vesicle'. The presence of an oval rather than a bipartite seminal vesicle is the critical feature distinguishing *Parahemiurus* from *Hemiurus* (see Gibson & Bray, 1979). Furthermore, Gaevskaja, who reported (1977) further specimens of this species in Baltic herring, noted *(in litt.)* that her specimens were similar to Rokicki's in terms of the seminal vesicle and possessed a larger sucker-ratio than that normally found in *H. luehei,* the usual hemiurid in herring. Nevertheless, she considered that they might be anomalous specimens of *H. luehei,* a suggestion with which we, after examining a specimen which she kindly gave us, strongly concur. A close examination of the latter specimen with DIC microscopy reveals an empty distal lobe of the seminal vesicle and shows that the pars prostatica is replete with spermatozoa.

Subfamily **DINURINAE** Looss, 1907

Stomachicolinae Yamaguti, 1958.

Diagnostic features. Ecsoma well developed; occasionally large. Body-surface plicated or smooth (apparently occasionally striated). Presomatic pit absent. Testes symmetrical to tandem; usually oblique. Seminal vesicle thin-walled; oval to tubular; may be constricted into two to four portions; in forebody, dorsal to ventral sucker or in hindbody. Pars prostatica tubular or vesicular; short or long; may be linked to seminal vesicle by aglandular duct. Sinus-sac present; small or large; usually oval; not enclosing ejaculatory (prostatic) vesicle. Permanent sinus-organ large and muscular, reduced to small papilla or apparently absent. Genital atrium usually well developed; deep or shallow (often depending upon contraction). Ovary usually oval; occasionally reniform or lobed. Terminal portion of uterus may or may not form distinct vesicle just outside sinus-sac. Vitellarium normally seven tubular lobes; three on one side, four on the other. Excretory arms united or not united in forebody. Normally parasitic in stomach of marine teleosts.

Genus ***DINURUS*** Looss, 1907

Diagnostic features. Body-surface with plications. Seminal vesicle tri-locular (or occasionally quadri-locular); in anterior hindbody or occasionally postero-dorsal to ventral sucker. Pars

prostatica long; may be densely or sparsely invested by gland-cells; linked to seminal vesicle by aglandular duct. Sinus-sac and permanent sinus-organ present; of variable size. Ovary oval. Excretory arms not united in forebody.

TYPE-SPECIES. *Dinurus contortus* (Rudolphi, 1819) [by original designation].

COMMENT. Although not recorded in our region, it is likely that *Dinurus* spp., occurring in fishes such as *Coryphaena* spp. and some of the other warm-water oceanic perciforms, do extend into the southern parts of our study-area. Indeed, Fischthal & Thomas (1972*a*) claim that *D. breviductus* Looss, 1907, has been reported in European Atlantic waters.

The relationships of the Atlantic forms of *Dinurus* were discussed by Gibson (1976). It is also worth noting that this author recorded a species of the related genus *Paradinurus* Vigueras, 1958, in a gempylid fish off the Canary Isles.

Genus *ECTENURUS* Looss, 1907

Magnacetabulum Yamaguti, 1934.
Parectenurus Manter, 1947.

DIAGNOSTIC FEATURES. Body-surface with plications. Seminal vesicle saccular, tubular or divided into two or three sections; postero-dorsal to ventral sucker or in anterior hindbody. Pars prostatica short (? or missing); connected to seminal vesicle by long, aglandular duct. Sinus-sac and permanent sinus-organ present; small. Ovary oval. Excretory arms not united in forebody.

TYPE-SPECIES. *Ectenurus lepidus* Looss, 1907 [by original designation].

Ectenurus lepidus Looss, 1907

Ectenurus trachuri Nikolaeva & Kovaleva, 1966, *nec* (Yamaguti, 1934) Yamaguti, 1970.
Ectenurus virgulus Linton of Parukhin *et al.* (1971) and Nikolaeva (1975).

TYPE-HOST AND LOCALITY. *Lichia amia,* Adriatic Sea at Trieste, Italy.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Trachurus trachurus [?] Kattegat off Frederikshaven, Denmark (Aug., 1976). Collected by M. Køie. BM(NH) 1983.12.14.1–2.
—— [stomach] Bay of Biscay (47°N, 06°W; Mar., 1980). BM(NH) 1983.12.14.3.

(b) From elsewhere
Metacercariae from *Sagitta tasmanica* [coelom] Off Atlantic coast of NW Africa (Feb., 1975; depth 200 m). Collected by C. Jarling. BM(NH) 1983.10.24.21.

(ii) NE Atlantic records from the literature
Trachurus trachurus [stomach] Aberdeen, Scotland (Sept., 1908). Nicoll (1913: 189).
—— [stomach] Off W of Scotland (July, 1954). Williams (1960: 708).
—— [?] ?NE Atlantic. Gaevskaja & Kovaleva (1980*a*: 53; 1982: 61).
—— [?] North Sea, Bay of Biscay, Straits of Gibraltar. Gaevskaja & Kovaleva (1980*b*: 19).

ASPECTS OF BIOLOGY. Little is known about the biology of this species; but we have identified metacercariae as occurring in a species of *Sagitta* (see above). This parasite does appear to be most common in the Mediterranean and Black Seas, but occurs in Atlantic waters of western Europe as far north as Scotland and Denmark, although it is not common, thus exhibiting a Lusitanean distribution. It is claimed to occur on the Atlantic coast of Africa as far south as Namibia (see below). In fact its distribution appears to coincide with that of its main host *Trachurus trachurus*. There have also been a fair number of records in the Mediterranean and Black Sea region from a wide range of fish, including *Lichia amia, Trachynotus ovatus, Atherina hepsetus, A. boyeri, Cepola macrophthalma, Pomatomus saltator, Lophius piscatorius, L. budegassa, Spicara maena, S. smaris, Scomber japonicus, Trachipterus trachypterus, Caranx rhonchus, Scyris alexandrina* and *Selar djeddaba*. *Ectenurus* spp. are generally considered to be parasites of

carangids. In the above list *Trachurus, Lichia, Trachynotus, Caranx, Scyris* and *Selar* are carangids, but *Cepola, Pomatomus* and *Spicara* are all related members of the Percoidei. Some hosts, e.g. *Lophius* spp., are presumably accidental, the worms having been taken in with their prey.

Previous descriptions. Looss (1908: 124; brief, but well illustrated); Vlasenko (1931: 118); Janiszewska (1953: 31; a few measurements only); Mazza (1963: 447; brief); Nikolaeva (1963: 410; brief, no figure; 1966: 53; some measurements only); Nikolaeva & Kovaleva (1966: 67; as *E. trachuri*).

Description. (Fig. 8). This description is based upon two flattened and one unflattened whole-mounts from fishes and two metacercariae from chaetognaths. As no sections were seen our interpretation is based upon these worms with occasional reference to the figures of Looss (1908). The measurements are given in Table 5.

The body-surface of these cylindrical to fusiform worms is almost entirely covered by shallow, transverse *plications*. They are absent from the ecsoma, but reach back laterally on the soma to a distance about half-way between the ovary and the posterior extremity of the soma. Ventrally they extend almost to the posterior limit and dorsally they reach to about the level of the ovary. These levels would be expected to vary with the state of contraction of the worm. In the forebody of flattened specimens the plications may not be visible, apart from the regions dorsally and laterally to the oral sucker. The ventral sucker is also surrounded by plications. In the metacercariae the plications are more easily seen and tend to extend further posteriorly. In all our specimens the *ecsoma* is everted, except in the case of the metacercariae where it is withdrawn and not fully formed. The *oral sucker* is small, with the result that the forebody is conical. It is ventrally subterminal and surmounted by an indistinct pre-oral lobe. In material fixed in formalin and other cold fixatives (with the exception of GAA and Berland's fluid) the anterior part of the body is usually curved ventrally, thus bringing the two suckers into close proximity and emphasizing the two muscular thickenings which occur dorso-laterally to the oral sucker (see Fig. 8B and the figures of Looss, 1908). In extended specimens without the ventral flexion of the body, these thickenings, which do appear to be a feature of the worm, can only be seen as oval patches of muscle just beneath the dorso-lateral surface of the body. Any protrusions caused by these muscular thickenings are probably transitory. There is a distinct pattern of papillae surrounding the aperture of the oral sucker visible in our unflattened specimens (Fig. 8E). The *ventral sucker* is very large and is normally within the anterior third of the body. The sucker-ratio is usually in the region of 1 : 2·5–3·5. As it is 1 : 2·5 in our smallest specimen, allometry may be involved.

There is no prepharynx. The muscular *pharynx* leads into a short, saccular oesophagus which appears to pass postero-laterally and join a commissure linking the two 'Drüsenmagen'. The caeca then pass posteriorly in the dorso-lateral fields and end blindly deep within the ecsoma when the latter is everted.

The excretory pore opens terminally on the ecsoma. According to our material, the first part of the stem of the Y-shaped *excretory vesicle* within the ecsoma (Fig. 8A) may be saccular with a 'papillate' lining, and the remainder of the stem appears to be tubular. According to Looss (1908) the stem divides at the level of the posterior margin of the ventral sucker, and the two arms end blindly lateral to the oral sucker. Although we have no sectioned material, our whole-mounts also indicate that the arms end blindly.

Two oval *testes* occur obliquely in the ventral field a short distance posterior to the ventral sucker. (Our unflattened whole-mount (Fig. 8D) is abnormal in that the anterior testis is very small and contains no stainable material.) The vasa efferentia cannot be seen in our specimens, but presumably they unite as they join the tripartite seminal vesicle, which occurs between the testes and the ventral sucker. The proximal and largest part of the seminal vesicle is globular to oval. It is separated by a constriction from the slightly smaller middle section, which is similarly shaped. The third part is tear-shaped and tapers distally to form a simple duct. The constriction between the middle and third parts is not always distinct. The aglandular duct is an unmodified region of the ejaculatory duct (often referred to as an aglandular region of the pars prostatica). It

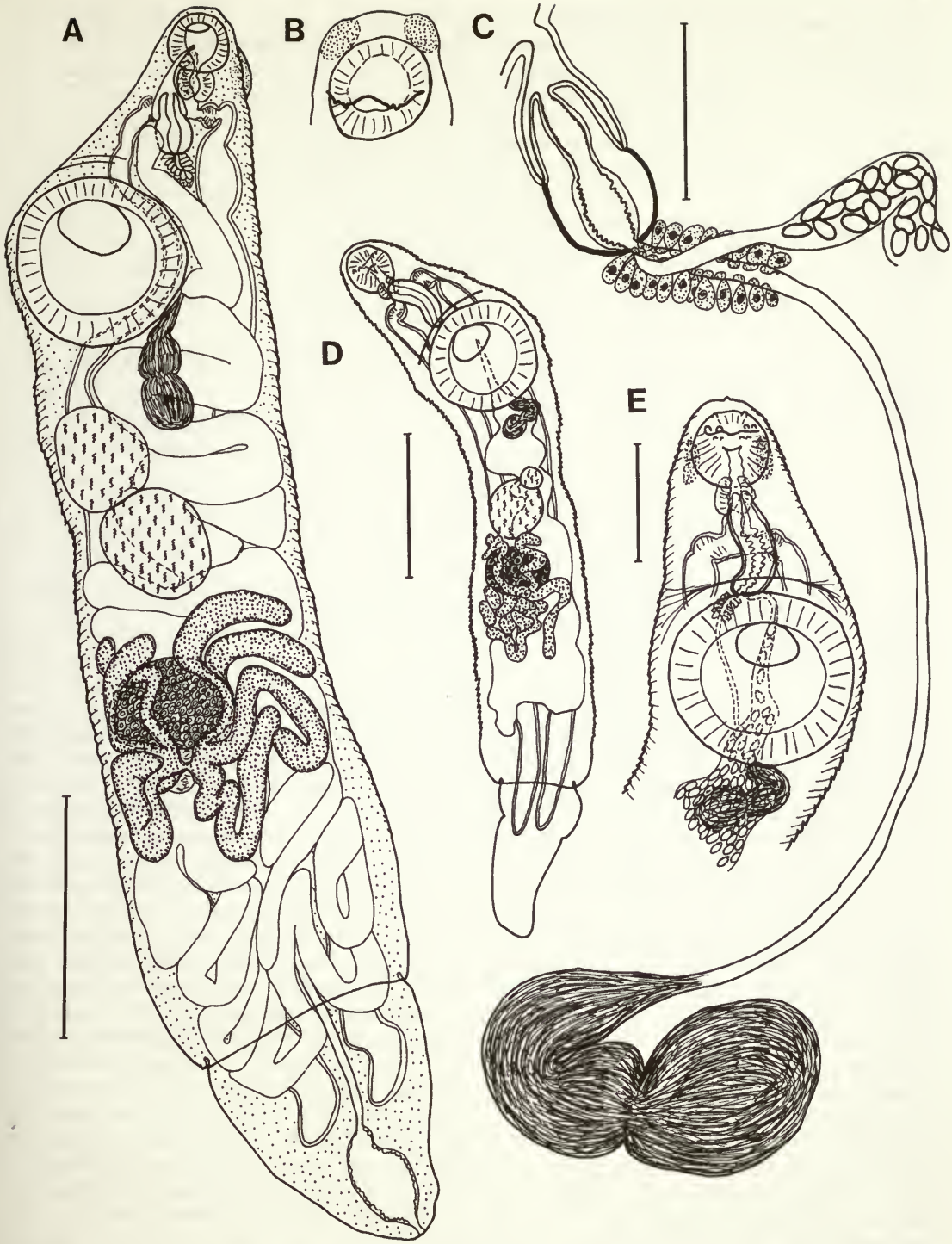


Fig. 8 *Ectenurus lepidus* ex *Trachurus trachurus*. (A) Flattened worm from Denmark; (B) Anterior extremity (curved ventrally) showing muscular pads; (C) Male terminal genitalia of flattened worm; (D) Small specimen from Bay of Biscay; (E) Anterior region of small specimen. Scale bars: A 500 μm; C 100 μm; D 200 μm; E 100 μm.

Table 5 Measurements of *Ectenurus lepidus*

Authority	Looss (1908)	Nikolaeva (1963)	Mazza (1963)	Present material
Host	*Lichia amia*	*Trachurus mediterraneus*	*Trachurus trachurus*	*Trachurus trachurus*
Locality	Trieste, Italy	Mediterranean	French Mediterranean	Kattegat
Length (mm)	up to 2·0	1·68–2·28	1·72	2·2–2·7
Breadth (mm)	0·25–0·3	0·31–0·34	0·41	0·5–0·6*
Ecsoma (mm)	–	–	–	0·45–0·5
Forebody (mm)	–	–	–	0·3–0·4
Oral sucker (mm)	0·08–0·12 diam.	0·7–0·11 × 0·08–0·11	0·09 × 0·07	0·12 × 0·11–0·13
Ventral sucker (mm)	0·2–0·3 diam.	0·17–0·22 × 0·2–0·32	0·29 diam.	0·35–0·36 diam.
Sucker-ratio	> 1 : 2	(1 : 3·4)	–	1 : 2·7–3·2
Testes (mm)	–	0·07–0·13 × 0·08–0·31	0·14 × 0·15	0·17–0·23 × 0·2–0·25
Ovary (mm)	–	0·12–0·13 × 0·13–0·16	0·1 × 0·14	0·13–0·2 × 0·21–0·26
Eggs (μm)	20 × 10	16–25 × 10–12	18–22 × 11–13	16–19 × 7–10 (usually 17–18 × 8–9)

Measurements in parentheses are calculated from figure.
*Flattened specimens.

is long and leads into the forebody dorsally to the ventral sucker. Inside the forebody the distal extremity of the duct forms a typical pars prostatica, i.e. it is surrounded by gland-cells and lined by anuclear blebs (Fig. 8C). The length of the pars prostatica in relation to the total length of the duct is difficult to judge in these specimens, but it must be in the range of 15–20 %. Although perhaps marginally wider than the remainder of the duct, the pars prostatica in our material is tubular and not vesicular, as figured by Looss (1908). Distally the pars prostatica opens into the base of a stout, oval to elongate oval sinus-sac, within which it immediately unites with the metraterm to form the hermaphroditic duct. The proximal region of this duct within the *sinus-sac* appears to have a thick, rugate or villous lining; but distally, where it passes through a stout, conical, permanent sinus-organ, it is a narrower, simple tube (this is more obvious in Looss' (1908) figures). The sinus-organ occurs within a deep genital atrium, which appears to open to the exterior mid-ventrally close to the ventral margin of the oral sucker. In the flattened specimens the sinus-sac, together with the sinus-organ, appears on superficial examination to form an oval structure ventrally in the forebody, which has a length similar to that of the oral sucker. In our unflattened specimen the sinus-sac is more elongate (Fig. 8D); but the sinus-organ is small. This difference may possibly be due to the relaxation of the muscles of the sinus-sac brought about by GAA fixation, as opposed to the contraction caused by formalin: hence the difference in size of the sinus-organ. It is important to remember that in worms like this, where the sinus-organ and sinus-sac are similar in size, the size of one must to some extent be a function of the size of the other. The position of the sinus-complex varies with the degree of contraction of the forebody and the genital atrium; but it normally occurs between the level of the anterior margin of the pharynx and the anterior margin of the ventral sucker.

The transversely oval *ovary* occurs ventro-laterally on either side of the body just anterior to the middle of the hindbody, although its position presumably depends upon the degree of contraction and the amount of evertion of the ecsoma. It may be slightly larger or slightly smaller than the testes, from which it is usually separated by loops of the uterus and/or lobes of the

vitellarium. The oviduct appears to leave the ovary postero-dorsally to join the Mehlis' gland – Juel's organ complex, which, although not clearly visible in our whole-mounts, appears to be similar to that of other hemiurids. The first coils of the *uterus,* immediately posterior to the latter complex, form a uterine seminal receptacle. The uterus then appears to loop back usually into the proximal region of the ecsoma, although not to the same extent as the caeca. It then loops forward on the side of the body opposite to the ovary past the ovarian complex, where it fills much of the available space in the remainder of the hindbody, often looping between the ovary and the hind-testis and passing dorsally to the testes. Dorsal to the ventral sucker it passes forward more directly, gradually narrowing, until it forms a narrow, tubular metraterm, which is of similar length to the pars prostatica, prior to entering the base of the sinus-sac where it unites with the male duct. The uterus is filled with numerous small, operculate eggs. The *vitellarium* is composed of seven digitiform lobes, which are arranged such that three lobes arise from one lateral collecting duct and four from the other. These short collecting ducts unite ventrally immediately posterior to the level of the ovary. The ducts are in fact so short that the seven lobes may appear superficially to have a rosette-like arrangement. The lobes are at least six times as long as they are wide, and occur in the ventral and lateral fields in the ovarian region, often crossing the ovary ventrally and lying between the ovary and the posterior testis (Fig. 8A, D). Presumably, a short common duct connects the transverse collecting ducts with the oviduct.

Discussion. *Ectenurus lepidus* is a parasite primarily of carangids, but it has been recorded from other groups of fishes, although mainly from members of the suborder Percoidei. Despite the fact that *Lichia amia* is the type-host, the majority of records have been from *Trachurus* spp. The only piscine host in the NE Atlantic, *Trachurus trachurus,* is unusual, when compared with the majority of teleosts in the region, in that it appears to have its own peculiar helminth-fauna.

According to the literature, *E. lepidus* has a widespread distribution outside European waters. In our opinion, however, this requires confirmation. Manter (1954), although noting that his specimens had a longer sinus-sac than that described by Looss (1908), claimed to have found it in *Helicolenus papillosus* (=*percoides*) and *Trachurus novaezelandiae* (possibly a synonym of *T. declivis*) in New Zealand waters. Manter believed that the 'short and thick' sinus-sac figured by Looss was 'in a contracted state'. The shape of the sinus-sac in our flattened, formalin-fixed material appears to be identical to that described by Looss. Until we obtained a small, unflattened specimen fixed in GAA, we believed that the short, broad sinus-sac was a distinctive feature of *E. lepidus*. We are now tending to believe that Manter's observation was correct, for, although this small specimen possesses a much more elongate sinus-sac, marginally larger eggs and a smaller sucker-ratio than our two flattened specimens, it appears to be within the limits of the species as described in the literature and possesses 'muscular thickenings' dorso-lateral to the oral sucker. We are, therefore, treating all of our specimens as being conspecific. In relation to Manter's New Zealand record, it is worth noting that Korotaeva (1975) did not find *E. lepidus* in *Trachurus declivis* in the Great Australian Bight, but claimed to have found *E. virgula* Linton, 1910, a species with a long sinus-sac. It is also worth mentioning that *E. antipodus* (Lebedev, 1968) has been recorded from a carangid, as has *E. helicoleni* (Lebedev, 1968) from *Helicolenus papillosus* in the Tasman Sea (the latter species is also claimed to occur in *Brama brama* off Mauritania – see Szuks, 1981).

Travassos *et al.* (1967) claimed to have found *E. lepidus* in *Oligoplites saurus* off the Atlantic coast of Brazil at Santa Cruz; but, according to their description, it has a long 'cirrus-sac' reaching to the posterior margin of the ventral sucker. In our opinion it more closely resembles *E. virgula*. A neighbouring species, *E. rodriguesi,* described by Cristofaro & Guimaraes (1974) from *Gymnothorax vicinus* appears to be a synonym of *Lecithocladium havanensis* (Vigueras, 1958). In our opinion, therefore, it seems unlikely that *E. lepidus* occurs on the western side of the North Atlantic. The common forms in the Gulf of Mexico are *E. virgula,* characterized by a very long, narrow sinus-sac, and *E. americanus* (Manter, 1947), a form similar to *E. lepidus,* but with a much smaller sucker-ratio. We have examined the specimens from *Caranx ruber* off Bermuda, which were designated *E. virgula* by Rees (1970), and consider them to be *E. americanus*. *E. chloroscombri* (Siddiqi & Cable, 1960) is very similar to, and probably synonymous with, *E. virgula*.

Both Manter & Pritchard (1960*b*) and Yamaguti (1970) claim that *E. lepidus* occurs in carangids off Hawaii. Manter & Pritchard noted that the sinus-sac is elongate and Yamaguti's figure clearly shows it to be quite a different shape to that of European specimens of *E. lepidus*. The Hawaiian form is similar to *E. selari* (Parukhin, 1966) from a carangid in the Gulf of Tonkin, which in turn is similar to *E. trachuri* (Yamaguti, 1934) *nec* Nikolaeva & Kovaleva, 1966, from a carangid off Japan. It is worth noting that *E. selari* and *E. trachuri* are very similar in morphology and occur in similar hosts to *E. virgula*, and that all three of these species are claimed to have been found off the Cape Verde Islands by Szuks (1981).

E. lepidus is also claimed to occur in carangids off the west coast of Africa by Kovaleva (1968*b*) [Namibia], Fischthal & Thomas (1971) [Ghana], Siddiqi & Hafeezullah (1975) [Nigeria] and Szuks (1981) [Cape Verde Islands and Mauritania]. Kovaleva recorded it from *Trachurus trachurus capensis*, but did not describe it. Fischthal & Thomas recorded it from *Chloroscombrus chrysurus*, *Decapterus rhonchus* and *Galeoides decadactylus*, and, although they gave no description, they compared it with specimens of *'E. lepidus'* from Hawaii, the material of Manter & Pritchard (1960*b*), and with the type-specimen of *E. chloroscombri*, which they consider synonymous with *E. lepidus* (but see above). They found all of this material to be 'basically alike'. Siddiqi & Hafeezullah (1975) provided a very brief description and a very small figure of one specimen from *Chloroscombrus chrysurus*. Although their specimen resembles *E. lepidus*, its description is not detailed enough for us to be certain of its identity; but the sinus-sac appears to be quite a different shape to that described for *E. chloroscombri* on the other side of the Atlantic. Szuks (1981) recorded *E. lepidus* from *Euthynnus alleteratus*, *Trachurus trecae*, *T. trachurus* and *Lutjanus agennes*, but did not describe or discuss the worms. He also quoted unpublished records from *Scomber japonicus* (=*colias*) and *Decapterus rhonchus* from off NW Africa.

In addition to the above records, Parukhin & Solonchenko (1967) briefly described, but did not figure, *E. lepidus* from *Selar crumenophthalmus* in the Gulf of Aden. Parukhin (1976*b*; 1978) also claimed to have found this species and *E. virgula* in the Gulf of Aden and *E. virgula* (spelled *vulgaris* in error in 1978) and *E. americanus* in other parts of the Indian Ocean. Parukhin & Solonchenko's description omits mention of the shape of the sinus-sac, so the worms' identity requires confirmation; but we have been able to confirm the presence of *E. virgula* in *Selar crumenophthalmus* in the Indian Ocean region from specimens from Pinang, Malaysia, housed in the collection of the BM(NH).

In 1931 Vlasenko described material from *Trachurus trachurus* (the fish may well have been *T. mediterraneus*, as only in recent years has this been recognized as a distinct species) in the Black Sea, which he thought were questionable specimens of *E. lepidus*. Vlasenko considered that they differed from *E. lepidus* of Looss (1908) in: (1) the shape of the vitellarium; (2) the length of the caeca; (3) the form and size of the ovary; (4) the absence of 'thickenings' lateral to the oral sucker; and (5) the ventral sucker being three times larger than the oral sucker. Although several workers, such as Osmanov (1940), Butskaja (1952), Pogorel'tseva (1952), Chernyshenko (1955) and even Kovaleva (1968 *a,b*), have continued to refer to specimens from the Black Sea as *E. lepidus*, Nikolaeva & Kovaleva (1966), Kovaleva (1969, 1970*a,b*) and Nikolaeva & Parukhin (1969) have considered that Vlasenko's material and their own specimens from *T. mediterraneus* were a distinct species, *E. trachuri* Nikolaeva & Kovaleva, 1966, *nec E. trachuri* (Yamaguti, 1934). They distinguished it from *E. lepidus* on: (1) the large size of the ventral sucker (ratio 1 : 3–4); (2) the ovary is larger than the testes rather than smaller; (3) the 'thickenings' lateral to the oral sucker are absent; and (4) the caeca extend well into the ecsoma. Later, Parukhin *et al.* (1971) and Nikolaeva (1975) considered this species to be a synonym of *E. virgula*. Nikolaeva distinguished it from *E. lepidus* by: (1) the small size of the pre-oral lobe; (2) the absence of 'thickenings' lateral to the oral sucker; (3) the large size of the ventral sucker; and (4) the large size of the ovary. In fact, the size and shape of the sinus-sac preclude any consideration of *E. trachuri* of Nikolaeva & Kovaleva (1966) as a synonym of *E. virgula*. In agreement with Fischthal & Thomas (1971), we consider it to be a synonym of *E. lepidus*, because many of the differences listed above can be considered within the range of intra-specific variation. The confusion results from the fact that Looss' description has been the only available detailed picture of *E. lepidus* (*sensu stricto*). Considering each of Nikolaeva's points in turn: (1) although their material does

appear to have a greater sucker-ratio than our material and that of Looss (1908), that of Mazza (1963) extends well into their range: in addition, one of our specimens has a ratio almost identical to that reported by Vlasenko (1931) and another is greater than 1 : 3; (2) the ovary in one of our two flattened specimens is larger than the testes; (3) the 'thickenings' lateral to the oral sucker would appear to be transitory or often inconspicuous; and (4) the caeca in our specimens extend well into the ecsoma.

Subfamily **ELYTROPHALLINAE** Skrjabin & Guschanskaja, 1954

Musculovesiculinae Skrjabin & Guschanskaja, 1954.

DIAGNOSTIC FEATURES. Ecsoma well developed. Body-surface smooth or plicated. Presomatic pit absent, but ventro-cervical groove often present. Testes tandem to symmetrical, usually oblique. Seminal vesicle with exceptionally thick, muscular wall; oval, not constricted into portions; in forebody, dorsal to ventral sucker or in hindbody. Pars prostatica tubular; long or short; usually linked to seminal vesicle by short, aglandular duct. Sinus-sac commonly tubular, long, not enclosing ejaculatory (prostatic) vesicle. Sinus-organ usually well developed, but delicate and amuscular. Genital atrium usually deep (depending upon contraction). Ovary oval. Eggs rarely filamented. Vitellarium seven tubular to tear-shaped lobes, three on one side, four on the other, which may form rosette. Excretory arms united in forebody. Parasitic mainly in stomach of marine teleosts.

Genus *LECITHOCLADIUM* Lühe, 1901

Magnapharyngium Bilqees, 1971.
Colletostomum Sahai & Srivastava, 1978.
Clefticolletta Sahai & Srivastava, 1978.

DIAGNOSTIC FEATURES. Body-surface with plications. Oral sucker often funnel-shaped. Pharynx elongate. Seminal vesicle large; in hindbody. Pars prostatica long and sinuous; mainly or entirely in hindbody. Sinus-sac tubular; narrow; not reaching level of seminal vesicle and usually entirely or mainly in forebody. Vitelline lobes long and tubular. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Lecithocladium excisum* (Rudolphi, 1819) [by original designation].

Lecithocladium excisum (Rudolphi, 1819) Lühe, 1901

Distoma excisum Rudolphi, 1819.
Fasciola excisum (Rudolphi) de Blainville, 1828.
Distoma (Crossodera) excisum (Rudolphi) Dujardin, 1845.
Distoma (Apoblema) excisum (Rudolphi) Stossich, 1886.
Apoblema excisum (Rudolphi) Juel, 1889.
Hemiurus excisus (Rudolphi) Looss, 1899.
Distoma (Lecithocladium) excisum (Rudolphi) Cohn, 1902.
Crossodera excisum (Rudolphi) Seurat, 1909.
?*Distomum crenatum* Molin, 1859.
?*Apoblema crenata* (Molin) Juel, 1889.
?*Lecithocladium crenatum* (Molin) Looss, 1907.
Lecithocladium excisiforme Cohn, 1903.
Distomum gulosum Linton of Johnstone (1906).
?*Lecithocladium 'exiguus'* of Radulescu (1969) [*nom. nud.* or *error pro 'excisum'*].

TYPE-HOST AND LOCALITY. *Scomber scombrus,* Rimini, Italy.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Scomber scombrus [stomach] Plymouth, Devon, England. Material of Baylis & Jones (1933: 631). BM(NH) 1932.12.6.10. Material collected by P. G. Corbin. BM(NH) 1937. 6.8.142–150.

—— [stomach] Off W of Scotland (56°N, 08°W; depth 120 m; July, 1954). BM(NH) 1959.10.14.26. (Material of Williams, 1960: 708).
—— [stomach] Off coast of Portugal (40°N, 10°W; depth 256–290 m; Jan., 1971). BM(NH) 1973.5.17.63–65. (Material of Bray, 1973: 178).
—— [stomach] Off Faeroe Isles (62°N, 08°W; July, 1976). BM(NH) 1983.12.14.4.
—— [stomach] Off St. Andrews, Scotland (July, 1949). Collected by D. D. R. Burt. BM(NH) 1983.12.14.5–8.
—— [stomach] Bay of Biscay (45°N, 02°W; depth 76–80 m; March, 1980). BM(NH) 1983.12.14.9.
Trachurus trachurus [?] Kattegat off Frederickshaven, Denmark. Collected by M. Køie. BM(NH) 1983.12.14.1–2.

(b) From elsewhere
(?) *Centrolophus niger* [stomach] Bordighera, Italy (removed from fish in BM(NH)). BM(NH) 1984.7.27.96 (=? *L. crenatum* (Molin)).
Scomber japonicus [stomach] Atlantic coast of Morocco (34°N, 09°W; depth 222–236 m; Jan., 1971). BM(NH) 1983.12.14.10.

(ii) NE Atlantic records from the literature
? *Scomber japonicus* [?] North or South Atlantic. Radulescu (1969: 80; as *'L. exiguus'*).
Scomber scombrus [stomach] Off Ireland. Bellingham (1844: 425; as *Distoma excisum*).
—— [intestine] (Rennes), Brittany, France. Dujardin (1845: 436; as *Distoma* (*Crossodera*) *excisum*).
—— [stomach] Varberg, Sweden (June, Aug., Sept.) Olsson (1868: 51; as *Distoma excisum*).
—— [stomach] Aalesund, Sweden. Olsson (1868: 51; as *D. excisum*).
—— [stomach] Bergen, Norway (Jul., Aug.). Olsson (1868: 51; as *D. excisum*).
—— [stomach] Bohuslän, Sweden (July). Olsson (1876: 21; as *D. excisum*).
—— [stomach & intestine] Belgian coast. van Beneden (1871: 37; as *D. excisum*).
—— [stomach & intestine] Kristineberg, Sweden. Juel (1889: 5; as *Apoblema excisum*); (July) Lönnberg (1889: 56; as *D. excisum*).
—— [?] Off Walney Island, Irish Sea (July, 1905). Johnstone (1906: 319; as *Distoma gulosum*).
—— [stomach] Millport, Firth of Clyde, Scotland. Nicoll (1910: 349).
—— [stomach] Aberdeen, Scotland. Nicoll (1913: 189).
—— [stomach] Plymouth, Devon, England. Nicoll (1914: 485); Baylis & Jones (1933: 631); Baylis (1939: 478).
—— [stomach] W of Scotland (June, 1954). Williams (1960: 708).
—— [stomach] Portugese coast (40°N, 10°W; depth 256–290 m; Jan., 1971). Bray (1973: 178).
—— [stomach] St Andrews, Scotland. Gordon, in Laverack & Blackler (1974: 35).
This species was also recorded probably just to the south of our region (the actual locality was not given) in *Scomber japonicus, S. scombrus, Trachurus trachurus* and *Caranx rhonchus* by Jessen (1975: 179).

Aspects of biology. Little is known about the biology of this species. The metacercariae probably occur in ctenophores and possibly other planktonic animals, as Boyle (1966) recorded five specimens of a species of *Lecithocladium* (he called it *L. excisum*: see below) from the ctenophore *Pleurobrachia pileus* in New Zealand waters and Reimer (1976) reported six records of a worm which he considered to be a species of *Lecithocladium* from *Pleurobrachia globosa* off Madras, India. Reimer (1976) also reported two other records in the same locality from *Janthina globosa*, a gastropod mollusc which lives on ctenophores and coelenterates.

The main host for the adult in our region is *Scomber scombrus*; but it also occurs in *S. japonicus*. There are also records in the literature from a wide range of other fishes outside our region; but, as discussed below, many of these records require confirmation. We have specimens from the carangid *Trachurus trachurus*, but they are immature. Looss (1908) also recorded immature forms from this host in the Mediterranean Sea, and a very low prevalence was reported by Parukhin *et al.* (1971) also from the Mediterranean. It is also said to occur in *Trachurus mediterraneus* from the Mediterranean and Black Seas (Nikolaeva, 1963; Nikolaeva & Kovaleva, 1966; Kovaleva, 1970*b*; Parukhin, 1976). It would appear, therefore, that while *Scomber* spp. are the main hosts, it may occasionally occur, often as an immature form, in other fishes, such as carangids, which occupy a similar ecological niche and which may feed on ctenophores. The distribution of *L. excisum* is dealt with in the 'Discussion'.

PREVIOUS DESCRIPTIONS. Dujardin (1845: 436; as *Distoma (Crossodera) excisum*; brief); Juel (1889: 8; as *Apoblema excisum*; parts of body only); Johnstone (1906: 319; as *Distoma gulosum*); Cohn (1903: 54; as *L. excisiforme*; brief); Looss (1908: 125; detailed figures); Markowski (1933: 18); Timon-David (1937: 16); Janiszewska (1953: 31; measurements only); Mazza (1963: 447; measurements and figures); Koval & Otsupok (1964: 50; measurements only); and Hadzhiiski (1980: 150; figure and a few measurements). It has also been described in the region of Japan by Yamaguti (1934: 479; measurements only); Zhukov (1960: 39; figure and a few measurements); and Ichihara *et al.* (1968: 49).

DESCRIPTION. (Figs 9 & 10). This description is based upon 21 whole-mounts and one obliquely sectioned specimen. The body is tubular, with a truncate anterior end and, usually, a conical posterior end, the latter being caused by the *ecsoma* which is usually protruded. The protruded ecsoma may comprise up to slightly more than half of the total length of the worm. In some specimens a double invagination of this organ may occur. Much of the somatic surface is covered with distinct annular *plications*; but these are absent on the ecsoma, ventrally between the suckers and surrounding the caudal extremity of the soma: they may extend slightly further posteriorly and be slightly more distinct on the ventral surface than on the dorsal. The plications are often quite widely spaced, especially on the dorsal surface, and they may be slightly crenulate. Dorsal to the pharynx is a distinct region where the plications are accentuated and much more deeply crenulate (Fig. 10A): this region is referred to by Looss (1908) as the 'Kräuselung' and is a very distinctive feature of this species, although it is not always visible in poorly fixed, frozen or flattened material. There is no sign of the muscular protrusion ('Nacken-buckel') dorsal to the oral sucker which is a distinctive feature of the related species *L. cristatum* (Rud., 1819) in unflattened material. There is no presomatic pit. Measurements of this species are given in Table 6.

The *oral sucker* is terminal, there being no pre-oral lobe; but the aperture may be oriented ventrally associated with a ventral flexion of the forebody. It is a large, muscular and infundibuliform organ, which is distinctly cleft on each ventro-lateral margin (Fig. 9A,B). The globular *ventral sucker* is smaller than the oral sucker: the ratio (width) is usually in the region of 1 : 0·8–0·9. In fully-developed worms it occurs within the first quarter of the soma, but in immature worms the forebody occupies a larger proportion of the body. The aperture of the ventral sucker tends to be oriented slightly antero-ventrally.

There is no prepharynx. the muscular *pharynx* is very large and elongate, often extending past the anterior margin of the ventral sucker. Posteriorly it gives rise to a short, oval and muscular oesophagus from which two relatively narrow, muscular arms arise dorso-laterally. These short ducts, which are lined with claviform, villous projections, pass antero-laterally to unite with the caeca. The latter gradually widen and almost immediately reflex and pass posteriorly, thus forming distinct 'shoulders'. There are no 'Drüsenmagen' visible in our material, although we have observed indistinct organs in the related *L. cristatum*. The relatively broad caeca pass back in the dorso-lateral fields and terminate blindly close to the distal extremity of the ecsoma.

The excretory pore is situated ventro-terminally on the ecsoma. The tubular, Y-shaped *excretory vesicle* has a smooth, vesicular lining and a muscular wall in the posterior region; but, in our sectioned specimen, at about one-third of the way along the ecsoma, the wall becomes very fluted, and about half-way along the ecsoma there is a distinct muscular sphincter, after which the vesicle has a more typical appearance. It continues forward medially into the soma between the coils of the uterus, running dorsally to the gonads, and bifurcates at about the level of the anterior margin of the anterior testis. The two arms continue forward in the dorso-lateral fields into the forebody, where they taper at about the level of the anterior half of the pharynx to become narrow ducts. In our sections these appear to gradually fade away; but Yamaguti (1934) claimed that in his live material and whole-mounts the arms were united dorsally to the oral sucker. Looss (1908) also found no connection between the ducts. Such a connection does normally occur in elytrophallines; but it is possible that in this instance the connecting duct, if present, is extremely fine.

The two oval *testes* occur almost symmetrically to tandem in about the middle of the soma, but their exact position varies considerably with the state of contraction or eversion of the ecsoma.

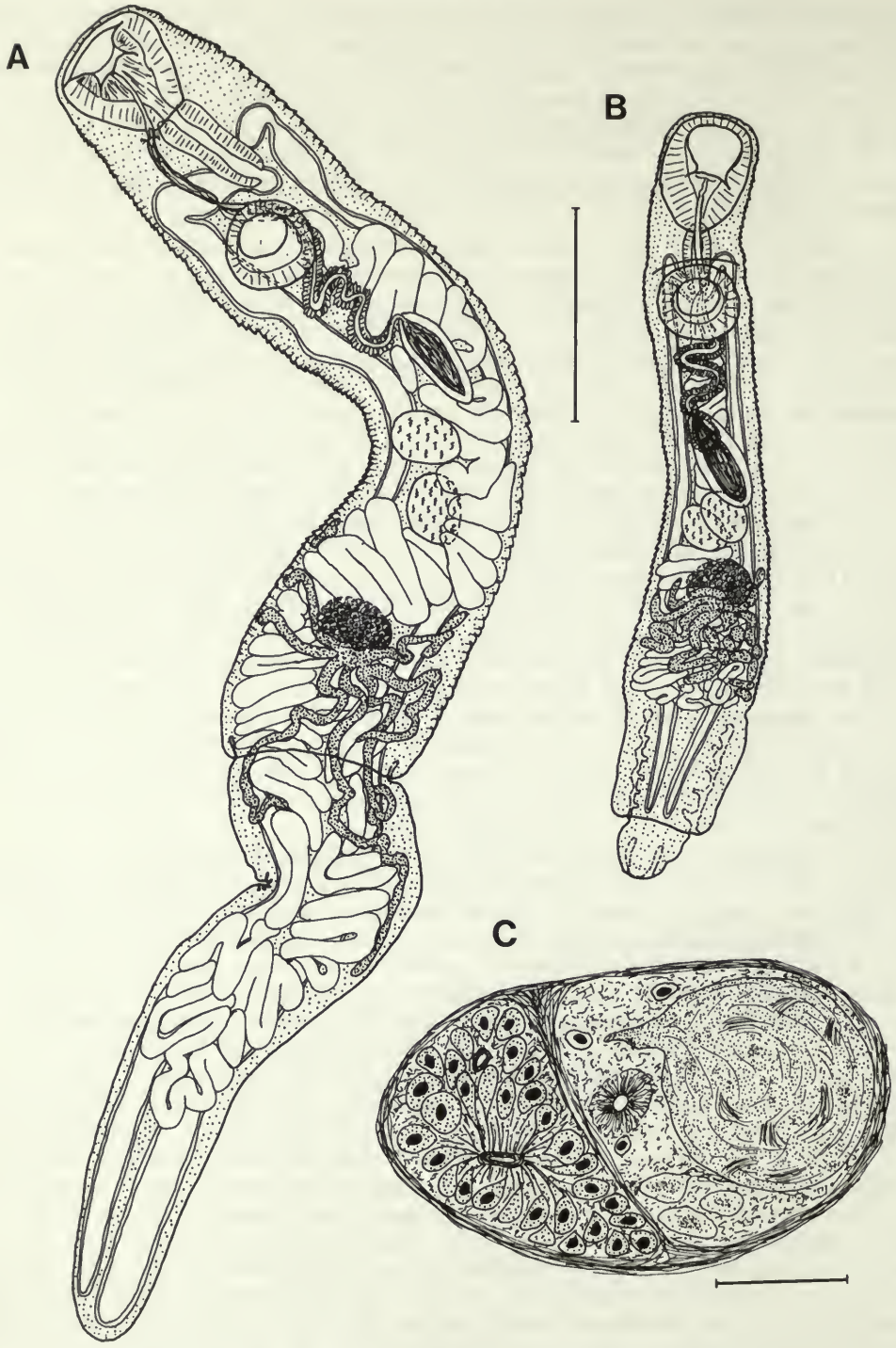


Fig. 9 *Lecithocladium excisum* ex *Scomber scombrus*. (A) Flattened worm; (B) Unflattened worm; (C) Section of Mehlis' gland – Juel's organ complex. Scale bars: A,B 1 mm; C 100 μm.

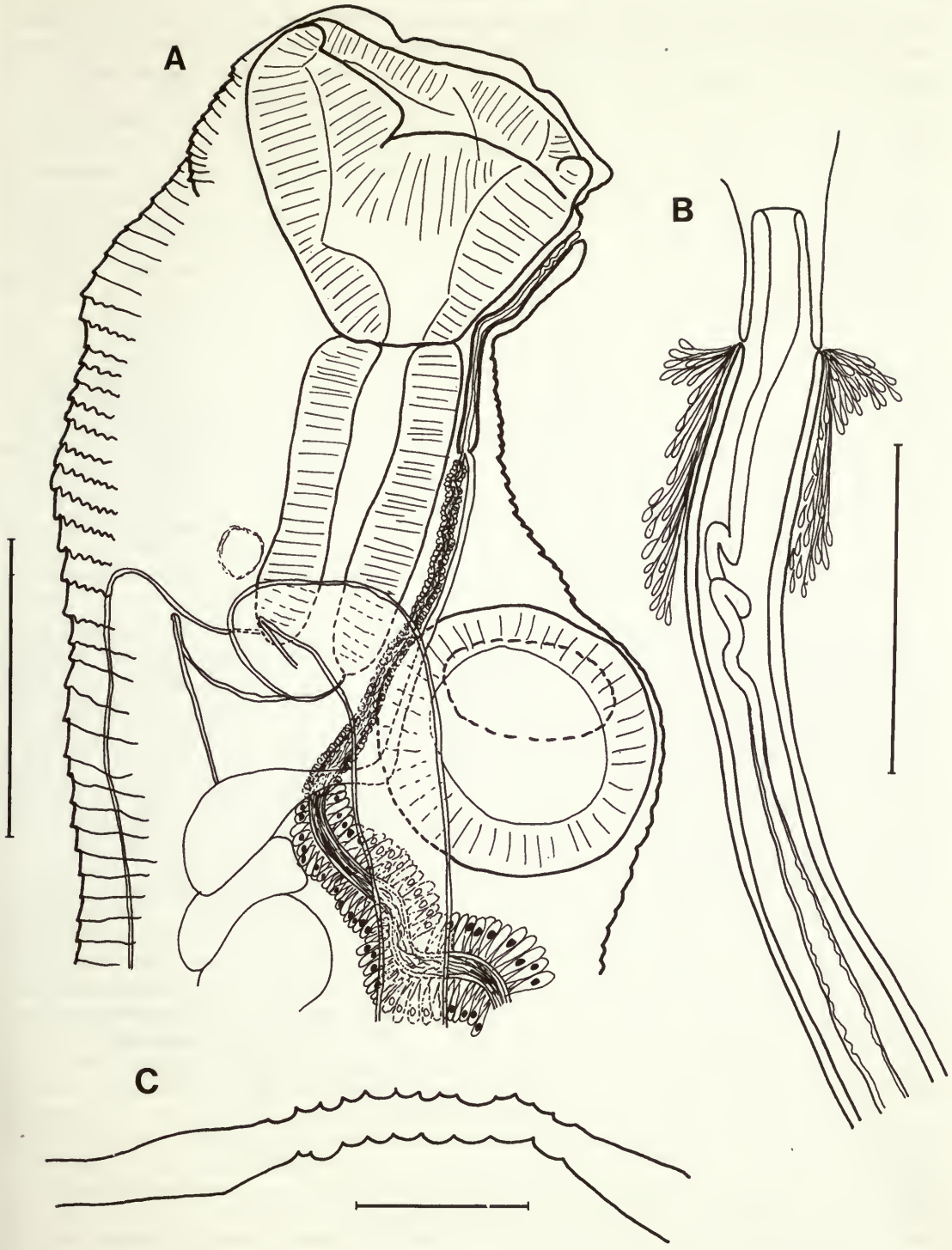


Fig. 10 *Lecithocladium excisum* ex *Scomber scombrus*. (A) Anterior region of laterally mounted, flattened worm; (B) Distal part of terminal genitalia; (C) Plications across surface dorsal to pharynx ('Krauselung'). Scale bars: A 500 μm; B 100 μm; C 200 μm.

Table 6 Measurements of *Lecithocladium excisum* from *Scomber scombrus*

Authority	Looss (1908)	Mazza (1963)	Koval & Otsupok (1964)	Present material
Locality	?Trieste, Italy	French Mediterranean	Black Sea	NE Atlantic
Length (mm)	3–8	2·92–4·85	5–8	3·5–7·2
Breadth (mm)	0·5–1	0·52–0·81	–	0·6–1·2
Ecsoma (mm)	–	0·64–1·03	–	0·15–4·0
Forebody (mm)	–	–	–	0·6–0·11
Oral sucker (mm)	0·65 × 0·5	0·1–0·14 × 0·31–0·48	0·33–0·63 × 0·37–0·67	0·35–0·65 × 0·38–0·6
Ventral sucker (mm)	0·35–0·45 diam.	0·23–0·34 × 0·26–0·35	0·33–0·49 × 0·35–0·56	0·3–0·47 × 0·35–0·5
Sucker-ratio	–	–	–	1 : 0·72–0·95
Testes (mm)	–	0·26–0·27 × 0·34–0·4	0·15–0·29 × 0·13–0·37	0·23–0·42 × 0·23–0·43
Ovary (mm)	–	0·24–0·33 × 0·17–0·26	0·13–0·27 × 0·33–0·35	0·15–0·3 × 0·28–0·39
Eggs (μm)	20–22 × 10–12	20–22 × 10–12	19–20 × 10–13	21–24 × 11–14 (usually 22–23 × 12–13)

When oblique, either the left or the right testis may be the more anterior, and the anterior testis is usually slightly more ventrally situated than the other. In our sectioned specimen the vasa efferentia are very short (c. 100 μm); but, judging by the variable position of the testes, they must be very contractile. They leave the testes anteriorly and unite almost immediately to form the seminal vesicle. This is a very large, fusiform structure with an extremely thick, muscular wall. It normally extends anteriorly from the testes obliquely to a level about half-way between the testes and the ventral sucker. The posterior extremity is usually more sinistrally and ventrally situated than the anterior extremity. Distally the seminal vesicle gives rise, via a short, aglandular duct, to the pars prostatica, which is very long. The proximal three-quarters of the pars prostatica in our material are broad, muscular, convoluted, surrounded by a dense, broad band of large gland-cells, and appear to possess a smooth lining and a lumen filled with spermatozoa. (It is worth noting that in *L. cristatum* the lining is more typical in that it bears the usual 'transitory' blebs which are assumed to arise from the outer gland-cells.) Most of this region of the pars prostatica occurs ventrally between the seminal vesicle and the ventral sucker. At about the level of the middle of the ventral sucker the pars prostatica straightens, narrows slightly, becomes relatively thin-walled, loses its broad band of external gland-cells and acquires a narrow, diffuse, external band of globular, non-staining cells (Fig. 10A). At this point a more typical lining develops, i.e. globular, non-staining blebs, which are often apparently ruptured. In this instance the typical external cells appear, therefore, to be physically separated from the internal blebs. This is difficult to explain, but it is possible that there are two kinds of cells in the pars prostatica of all hemiurids and that it is the small, non-staining cells that form the internal blebs. As there is no evidence of the blebs in the proximal part of the pars prostatica, it is unlikely that they have migrated down the duct. In the posterior forebody or often antero-dorsally to the ventral sucker in smaller worms, the pars prostatica unites with the metraterm as they enter the base of the sinus-sac. The length of the narrow, cylindrical *sinus-sac* varies, usually being longer than the pharynx in small worms and slightly shorter in large worms. Its position is also variable due to the fact that the wall of the genital atrium is very contractile, so the position of its posterior extremity varies between a level antero-dorsal to the ventral sucker and just anterior to the middle of the pharynx. The anterior extremity of the sinus-sac is often very difficult to elucidate, as in many whole-

mounts it appears to grade into the wall of the genital atrium. One feature which indicates the whereabouts of the junction between the wall of the sinus-sac and that of the genital atrium is a bunch of small gland-cells which surround it (Fig. 10B): this feature was also noted by Gibson (1976) in the related *L. cristatum* and *Elytrophalloides oatesi* (Leiper & Atkinson, 1914). Within the sinus-sac the hermaphroditic duct is initially straight or sinuous, but the distal third of its length may be much more sinuous or slightly convoluted. Within the genital atrium the hermaphroditic duct is everted to form a small, amuscular sinus-organ (Fig. 10B); but this is very difficult to see in many specimens. It is possible that it is a temporary feature in this species, but it is likely, as in other members of the subfamily, that it is very variable in size. The genital atrium is very variable in length, but its junction with the sinus-sac is usually ventral to the oral sucker. The genital pore occurs mid-ventrally immediately posterior to the ventral margin of the oral sucker.

The oval *ovary* occurs mid-ventrally in the posterior half of the somatic hindbody, usually being separated from the testes by loops of the uterus. Even in our most extended specimens the ovary does not penetrate the ecsoma. Immediately posterior to the ovary, Juel's organ and Mehlis' gland form a large, oval complex which is distinctly delimited from the surrounding parenchyma by a layer of connective tissue (Fig. 9C). Juel's organ includes a large 'inner vesicle' containing many spermatozoa, which has caused several authors to consider it to be a seminal receptacle. The short oviduct leaves the ovary postero-medially, enters the proximal female complex and almost immediately receives the duct from Juel's organ and the common vitelline duct. The oötype is tubular and winds through the mass of gland-cells which form Mehlis' gland. On leaving the complex the first coils of the *uterus* are filled with spermatozoa and thus form a uterine seminal receptacle. The initial coils loop posteriorly, extending deep into the ecsoma, although not nearly as far as the caeca. In specimens with a withdrawn ecsoma the uterine coils may be retained in the soma (Fig. 9B). The coils then reflex and return anteriorly mainly on the opposite side of the body to that in which they have descended, passing laterally to the ovary, but extending across the body between the ovary and the testes. The coils then tend to run dorsolaterally to the testes on the opposite side of the body to that on which they passed the ovary and then fill much of the region dorsal to the seminal vesicle and pars prostatica. Dorsally or posterodorsally to the ventral sucker the uterus tapers to form a narrow, muscular metraterm, which continues forwards directly to unite with the male duct as they pass through the base of the sinus-sac. The uterus is filled with numerous small, operculate eggs. Occasionally spermatozoa may be seen filling portions of the distal uterus.

The *vitellarium* is composed of seven long, tubular lobes which unite postero-ventrally to the ovary and ventrally to the Mehlis' gland – Juel's organ complex. The lobes, which are arranged with three on one side of the body and four on the other, extend around the worm in the dorsolateral fields, reaching between the levels of the posterior margin of the testes and the middle of the ecsoma.

Discussion. *Lecithocladium excisum* was first recorded by Rudolphi (1819) from *Scomber scombrus* at Rimini on the Adriatic coast of Italy and from *S. japonicus* at Naples. Subsequently, it has been recorded frequently from these fishes, in particular *S. scombrus,* from the Mediterranean and Black Seas and the NE Atlantic region as far north as the Faeroes. Records from other parts of the world require confirmation. Those from the NW Atlantic (Linton, 1901, 1940; Nahhas & Short, 1965; Nahhas & Powell, 1971) are mainly from stromateid fishes and are based on *Distomum gulosum* Linton, 1901, which we believe more closely resembles *L. cristatum* (Rudolphi, 1819) than *L. excisum.* The records from the Atlantic coast of Africa all lack descriptions and in many cases the hosts listed suggest the possibility that other species are involved. Records include Solonchenko (1966, 1968) from *Scomber japonicus* off Namibia, Fischthal & Thomas (1971) from *S. japonicus* and several non-scombrid hosts off Ghana, Fischthal & Thomas (1972*a*) from *Arnoglossus imperialis* off Senegal, and Siddiqi & Hafeezullah (1975) from a stromateid and a polynemid off Nigeria. In 1971 Fischthal & Thomas also described two new species, *L. mecoderum* and *L. unibulbolabrum,* from a polynemid and a dactylopterid, respectively, from off Ghana, and in 1980 Fischthal claimed to have found the latter species in *S. japonicus* in the eastern Mediterranean. In view of this, all of the African records of *L. excisum*

can at present be considered questionable, and many are perhaps more likely to belong to *L. cristatum* which occurs in stromateids and *Arnoglossus* (see below) and closely resembles Fischthal & Thomas' (1971) description of *L. unibulbolabrum*.

Non-Atlantic records of *L. excisum* include several Pacific and Indian Ocean reports. Manter (1954) claimed to have found immature specimens in *Caesioperca* and *Paraperca* off New Zealand, and Boyle (1966) followed Manter's identification when he reported a metacercaria in *Pleurobrachia pileus* also in New Zealand waters. In Australian waters Korotaeva (1974) claimed to have found *L. excisum* in *Scomber australasicus* and *Rastrelliger kanagurta*, but gave no description. Our observations of material from the latter host from off Malaya and South Africa suggest that Korotaeva's material may have been one of the Indo-Malaysian species, such as *L. angustiovum* Yamaguti, 1953. Records from the Gulf of Tonkin and South China Sea (Oshmarin, 1965; Lebedev, 1970; Mamaev, 1970), mainly from carangids, suggest, judging from Oshmarin's brief description, that this material would be better accommodated in one of the very confused Indo-Malaysian species, such as *L. megalaspis* Yamaguti, 1953 (see Table 7).

More convincing records of *L. excisum* are those of Layman (1930), Yamaguti (1934), Zhukov (1960), Ichihara *et al.* (1968), Machida *et al.* (1970, 1972) and Ichihara (1974), mainly from *S. japonicus*, but also from a wide range of other hosts, in the Sea of Japan and other Japanese waters. Only Yamaguti (1934), Zhukov (1960) and Ichihara *et al.* (1968) give descriptions; but none is detailed enough to permit a confident identification, although they do resemble *L.*

Table 7 The relationship of *Lecithocladium* spp. of the Indo-Malaysian region

Group	Species	Main hosts	Features
A	*L. angustiovum* Yamaguti, 1953 Syns: *L. scombri* Yamaguti, 1953 *L. bulbolabrum* Reid, Coil & Kuntz, 1966 *L. unibulbolabrum* Fischtal & Thomas of Al-Yamani & Nahhas (1981)	Scombrid genus *Rastrelliger*	Up to 4 mm in length; oral sucker much larger than ventral sucker; eggs 16–22 μm
B	*L. apolecti* Velasquez, 1962 Syns: ? *L. annulatum* Chauhan, 1945 *L. excisiforme* of Gupta & Sehgal (1971) *L. psenopsis* Yamaguti of Bilqees (1981) *L. hexavitellarii* (Bilqees, 1971) *L. anteporus* (Bilqees, 1971) *L. tetravitellarii* (Bilqees, 1971) *L. microductus* (Bilqees, 1971) *L. arabiana* (Bilqees, 1971) *L. octovitellarii* (Bilqees, 1971) *L. microcaudum* (Bilqees, 1971) *L. stomatei* Farooq & Khanum, 1980	Stromateids, especially *Stromateus* and *Formio niger*	Up to 14 mm in length; oral sucker much larger than ventral sucker; eggs 9–14 μm
C	*L. parviovum* Yamaguti, 1953 Syns: ? *L. annulatum* of Gupta & Seghal (1970) *Cleftocolleta magnum* Sahai & Srivastava, 1978	Mainly *Rastrelliger*, carangids and ? stromateids	Up to 12 mm in length; oral sucker larger than ventral sucker; eggs 13–19 μm

Table 7 *continued*

Group	Species	Main hosts	Features
	L. keralense Gupta & Gupta, 1978 *L. indicum* Gupta & Gupta, 1978 ? *L. elongatus* Gupta & Puri, 1982 ? *L. srivastavai* Gupta & Puri, 1982 ? *L. stromateusi* Gupta & Puri, 1982 ? *L. sciani* Gupta & Puri, 1982 ? *L. pampi* Lebedev of Gupta & Puri (1982) ? *L. fotedari* Gupta & Singh, 1983		
D	*L. megalaspis* Yamaguti, 1953 Syns: ? *L. angustiovum* of Fischthal & Kuntz (1964) *L. dawesi* Bashirullah & D'Silva, 1973 *L. inglisi* Gupta & Ahmad, 1977 *L. purense* Gupta & Gupta, 1978 ? *L. arabicum* Farooq & Khanum, 1980 ? *L. singhi* Gupta & Singh, 1983	Mainly carangids	Up to 4 mm in length; suckers similar in size; eggs 16–26 μm (usually 20–24 μm)
E	*L. glandulum* Chauhan, 1945 Syns: *L. carultum* Chauhan, 1945 *L. triacantha* Gupta & Gupta, 1978 *L. thapari* Gupta & Gupta, 1978 ? *L. psettodi* Gupta & Puri, 1982 ? *L. manteri* Gupta & Puri, 1982	Variety of hosts, especially sciaenids	Up to 6 mm in length; suckers similar in size or ventral sucker slightly larger; eggs 20–23 μm
F	*L. harpodontis* Srivastava, 1937 Syns: ? *Clupenurus piscicola* Srivastava, 1935 *L. brevicaudum* Srivastava, 1937 *L. ilishae* Mamaev, 1970, *nec* Bashirullah & D'Silva, 1973 *L. ilishae* Bashirullah & D'Silva, 1973, *nec* Mamaev, 1970 *L. chauhani* Hafeezullah, 1975 *Colletostomum muthiahi* Sahai & Srivastava, 1978	Variety of hosts, including the clupeid *Hilsa*	Up to 6 mm in length; suckers similar in size or ventral sucker slightly larger; eggs 12–20 μm
G	*L. karachii* Zaidi & Khan, 1977 Syns: *L. pakistanensis* Zaidi & Khan, 1977 ? *L. magnetacetabulum* Yamaguti of some authors	Carangids	Up to 5 mm in length; ventral sucker much larger than oral sucker; eggs 15–20 μm

excisum. The records from *S. japonicus* suggest that the identifications may be reliable, especially as the latitude of their recovery is similar to that of the NE Atlantic. The presence of *L. excisum* in this region does, however, require confirmation.

Zhukov (1977) maintained that several species of *Lecithocladium* from the Indian coast, described by Srivastava (1937, 1942) and Chauhan (1945), are synonyms of *L. excisum*. The Indo-Malaysian region contains numerous nominal *Lecithocladium* species, many poorly described and all in a state of confusion. A study of the literature has revealed that little account has been taken of intra-specific variation, fixation artifacts or functional variation in the erection of these numerous taxa. In Table 7 we have attempted to bring some semblance of order by reducing the more than forty nominal species to only six, and some of the latter are very similar to each other. We hope that this drastic action will, at least, provoke further critical investigation and make at least some sort of reasonable identification of Indo-Malaysian forms possible. The most similar species to *L. excisum* in Table 7 are *L. angustiovum* Yamaguti, 1953 and *L. parviovum* Yamaguti, 1953. Specimens in the Collection of the BM(NH) identified as *L. angustiovum* from *Rastrelliger kanagurta* off Pinang, Malaysia, can be distinguished from *L. excisum* by their much smaller size. *L. parviovum* differs from *L. excisum* in its markedly smaller eggs. As indicated in Table 7, we are doubtful whether *L. excisum* occurs in the Indian Ocean.

Several authors (Dawes, 1947; Nahhas & Short, 1965; Fischthal & Thomas, 1971; Zhukov, 1977) list *L. cristatum* as a synonym of *L. excisum*, despite Looss' (1908) clear descriptions. We regard *L. cristatum* as distinct for the reasons given by Gibson (1976), and, incidentally, doubt the validity of *L. falklandicum* Gaevskaja & Kovaleva, 1978, a new name for *L. cristatum* of Gibson (1976). *L. cristatum* has not been recorded in the NE Atlantic; but, as it is known to occur in stromateids, it may be present in *Stromateus fiatola* in the south of the region. It is worth noting that in the Collection of the BM(NH) there are specimens which, in possessing a distinct 'Nacken-buckel', are clearly identifiable as *L. cristatum*. They are believed to have come from a species of *Arnoglossus* in the Mediterranean Sea. Fischthal & Thomas (1972*a*) recorded *'L. excisum'* from *Arnoglossus* off Senegal, and, from another west African locality, Ghana, these authors (1971) described a species, *L. unibulbolabrum*, possessing a 'Nacken-buckel' and closely resembling *L. cristatum*. As mentioned above, Fischthal (1980) recorded *L. unibulbolabrum* from several hosts in the Mediterranean Sea, so it seems likely that this species can be considered a synonym of *L. cristatum*. Consequently, bearing in mind our earlier comments on *D. gulosum*, it would appear that *L. cristatum* has a much wider distribution than previously believed. *L. mecoderum* Fischthal & Thomas, 1971, may also be a synonym of *L. cristatum*.

We have included *L. crenatum* (Molin, 1859) as a questionable synonym of *L. excisum*, although Looss (1908) considered that it was possibly a valid species. Molin (1859) described it from *Centrolophus niger* at Padua, Italy, claiming to have found over 100 specimens. Apart from nine specimens reported by Looss (1908) from Trieste, Italy, there are no further records of *Lecithocladium* spp. from this host. Molin's figure resembles *L. excisum*, although the host (a stromateoid) and Looss' comments suggest the possibility of a closer relationship with *L. cristatum*. We have recovered some poorly preserved and contracted specimens of *Lecithocladium* from a specimen of *C. niger* from Bordighera, Italy, now housed in the Fish Collection of the BM(NH). In having the oral sucker significantly larger than the ventral and in having eggs of 20–25 μm in length, these worms resemble *L. excisum*, and are herein considered to indicate that *L. crenatum*, although found on the other side of Italy, is possibly a synonym of *L. excisum*.

The distribution of *L. excisum* can, therefore, be definitely stated as including the Mediterranean and Black Seas and the NE Atlantic region. Whether or not it occurs in Japanese waters needs further investigation; but it seems unlikely that it is the widespread species which an uncritical examination of the literature would suggest.

Subfamily **GLOMERICIRRINAE** Yamaguti, 1958

DIAGNOSTIC FEATURES. Ecsoma well developed. Body-surface plicated. Pre-somatic pit absent. Testes oblique to tandem. Seminal vesicle bipartite; both parts globular to spindle-shaped; anterior part muscular; in hindbody or dorsal to ventral sucker. Pars prostatica tubular; short;

linked to seminal vesicle by aglandular duct. Oval sinus-sac present; in hindbody, dorsal to ventral sucker or occasionally in forebody; enclosing glandular ejaculatory vesicle. Hermaphroditic duct convoluted. Sinus-organ present; amuscular; long; convoluted. Genital atrium well developed; long and wide proximally. Vitellarium two irregularly oval to indistinctly lobed, symmetrical masses. Excretory arms united in forebody. Parasitic in stomach of marine teleosts.

Genus *GLOMERICIRRUS* Yamaguti, 1937

DIAGNOSTIC FEATURES. As subfamily.

TYPE SPECIES. *Glomericirrus amadai* Yamaguti, 1937 [by original designation].

Glomericirrus macrouri (Gaevskaja, 1975) Gaevskaja, 1979

'Genus novum D, species nova' of Armstrong (1974).
Hemiurus macrouri Gaevskaja, 1975.
? *Dinosoma* sp. of Zubchenko (1975).
Glomericirrus n. sp. of Haedrich & Polloni (1976).
Glomericirrus ulmeri Campbell & Munroe, 1977.

TYPE-HOST AND LOCALITY. *Coryphaenoides rupestris*, northern North Mid-Atlantic Ridge.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Coryphaenoides rupestris [stomach] W of the Faeroes (62°N, 11°W; depth 820-860 m; June, 1974). BM(NH) 1983.12.12.1–2.
—— [stomach] SW of Rockall (56°N, 17°W; depth 640 m; June, 1974). BM(NH) 1983.12.13.3–4.
—— [stomach] Off St. Kilda (58°N, 10°W; depth 820–825 m; Oct., 1978) BM(NH) 1983.12.13.5; (depth 990–1000 m; Oct., 1978) BM(NH) 1983.12.13.6.
—— [stomach] Off Flannan Island, W Scotland (59°N, 08°W; depth 900–920 m; Oct., 1978). BM(NH) 1983.12.13.7.
Hoplostethus atlanticus [stomach] Rosemary Bank, W of Scotland (59°N, 11°W; depth 970–1025 m; June 1974). BM(NH) 1983.12.13.8.
Nezumia aequalis [stomach] Off Tory Island, NW Ireland (55°N, 10°W; depth 880–1000 m; June, 1974). BM(NH) 1983.12.13.9.
Trachyrincus trachyrincus [stomach] WNW Sulisker (Sula Sgeir), NW Scotland (59°N, 08°W; depth 1120–1140 m; Apr., 1973). BM(NH) 1983.12.13.10.
—— [stomach] Off St. Kilda (58°N, 10°W; depth 1300–1320 m; Oct., 1978). BM(NH) 1983.12.13.11.

(b) From elsewhere
None.

(ii) NE Atlantic records from the literature
Coryphaenoides rupestris [stomach] Northern North Atlantic Ridge. Gaevskaja (1975: 458; as *Hemiurus macrouri*; 1979: 269); Zubchenko (1981*a*: 28).
(?)—— [stomach] North Atlantic. Zubchenko (1975: 235; as *Dinosoma* sp.).
(?) *Macrourus berglax* [stomach] North Atlantic, Zubchenko (1975: 235; as *Dinosoma* sp.).

ASPECTS OF BIOLOGY. Virtually nothing is known about the biology of this species. For the present we are restricting our concept of the species to forms from macrourids and neighbouring deep-water fishes, although it is possible that future work may show that it also occurs in some coastal flatfishes. Definite records of this species indicate that it occurs in a wide range of macrourids on both sides of the North Atlantic on the edge of the continental shelf and on the Northern Mid-Atlantic Ridge at depths of mainly between 500 and 2000 metres, although it is possible that Campbell & Munroe (1977) obtained material from below these depths. On the western side of the North Atlantic (see Armstrong, 1974; Campbell & Munroe, 1977; Campbell *et al.*, 1980; Zubchenko, 1981*b*; Campbell, 1983) its range extends into the Gulf of Mexico. In addition, it has also been recorded in the South Atlantic in the region of the Falkland Isles (Gaevskaja & Rodjuk, 1983), in the sub-Antarctic region (Rodjuk, 1981) and off Angola and Namibia (Gaevskaja &

Aleshkina, 1983). Whether or not it occurs off Japan requires further study (see below). In addition to macrourids, we have also found it in the trachichthyid fish *Hoplostethus atlanticus*, which until recently was virtually unknown in the NE Atlantic. This fish is now known to occur in relatively large numbers in the same bathyal habitat as the macrourids on the edge of the continental shelf as far north as Flannan Island off the NW coast of Scotland (Bridger, 1978; as *Gephyroberyx darwini*: see Merrett & Wheeler, 1983).

PREVIOUS DESCRIPTIONS. Armstrong (1974: 142; as 'Genus novum D, species nova'); Gaevskaja (1975: 458; as *Hemiurus macrouri*; 1979: 269; terminal genitalia only); Campbell & Munroe (1977: 285; as *G. ulmeri*).

DESCRIPTION (Fig. 11). The body of this relatively small worm is fusiform; but widest at the level of the ventral sucker, which protrudes considerably, making it difficult to mount specimens dorso-ventrally, and at the level of the vitellarium (Fig. 11A). The *ecsoma* may be withdrawn or extend up to about half the length of the soma (or to as long as the soma according to Gaevskaja, 1975). It is most usually withdrawn in poorly preserved material. Most of the body-surface, with the exception of the ecsoma, is covered with annular *plications*. These reach posteriorly to a level just anterior to the posterior extremity of the soma in the ventral field, to about the level of the vitellarium in the lateral fields and to about the level of the testes in the dorsal field. In addition, plications are absent or reduced to minute corrugations mid-ventrally in the forebody. The plications are slightly crenulate, often more distinctly so than in *Brachyphallus crenatus*, but normally less so than in *Dinosoma* spp. The *oral sucker* is ventrally subterminal and surmounted by an insignificant pre-oral lobe. The forebody is short, conical and concave ventrally. The *ventral sucker* is very large, the sucker-ratio being within the range of 1 : 2–3. It is round, protrudes significantly and the lumen tends to be oriented antero-ventrally (Fig. 11A). The measurements of this species are given in Table 8.

There is no prepharynx, the oral sucker opening directly into a muscular, oval *pharynx*. This in turn opens posteriorly in our sectioned material into a short, muscular oesophagus, which almost immediately bifurcates to form two short, postero-laterally oriented ducts that open into a small pair of 'Drüsenmagen', each with a muscular wall and a coarse, villous lining. These in turn open into the caeca-proper which extend posteriorly in the dorso-lateral field and terminate blindly normally within the ecsoma and occasionally close to its posterior extremity. One caecum may extend considerably further posteriorly than the other.

The excretory pore is situated ventro-terminally on the ecsoma. This opens into a short section of the *excretory vesicle* of variable width (but often very dilate), which extends about one-quarter of the length of a well-protruded ecsoma. This is very similar to the situation in *Brachyphallus crenatus*, except that this region has no distinct villous lining. It is separated from the rest of the stem of the vesicle by a distinct valve. The narrow stem continues forward mid-ventrally into the soma and then passes antero-dorsally past the ovarian complex into the mid-dorsal field at the level of the posterior testis. In our sectioned material, the vesicle bifurcates at this level and the two, narrow arms run forward ventro-laterally to pass on either side of the seminal vesicle. The arms continue into the forebody in the lateral fields and unite dorsally to the pharynx.

The two subglobular *testes* occur obliquely and contiguously or close together roughly half-way between the ventral sucker and the ovary, although their position and size are variable. The posterior testis tends to be on the same side of the body as the ovary, and both testes tend to occur in the ventro-lateral fields, although one is often more dorsal than the other. Occasionally, the testes occur almost in tandem. The short vasa efferentia leave the testes antero-dorsally and, in our sectioned specimens, pass dorsally to enter the seminal vesicle. Although they appear to unite as they pass into the wall of the seminal vesicle, this union is not clear in our sections. The seminal vesicle is bipartite. The two parts are variable in size, depending upon the amount of spermatozoa that they contain, and are frequently larger than the testes. Although the proximal part is usually the smaller, this is not always so. Both parts tend to be oval, but the proximal part has a thin wall, while the distal part is characterized by having a very thick, muscular wall similar to that of the seminal vesicle of elytrophalline hemiurids (Fig. 11B). The narrow union between

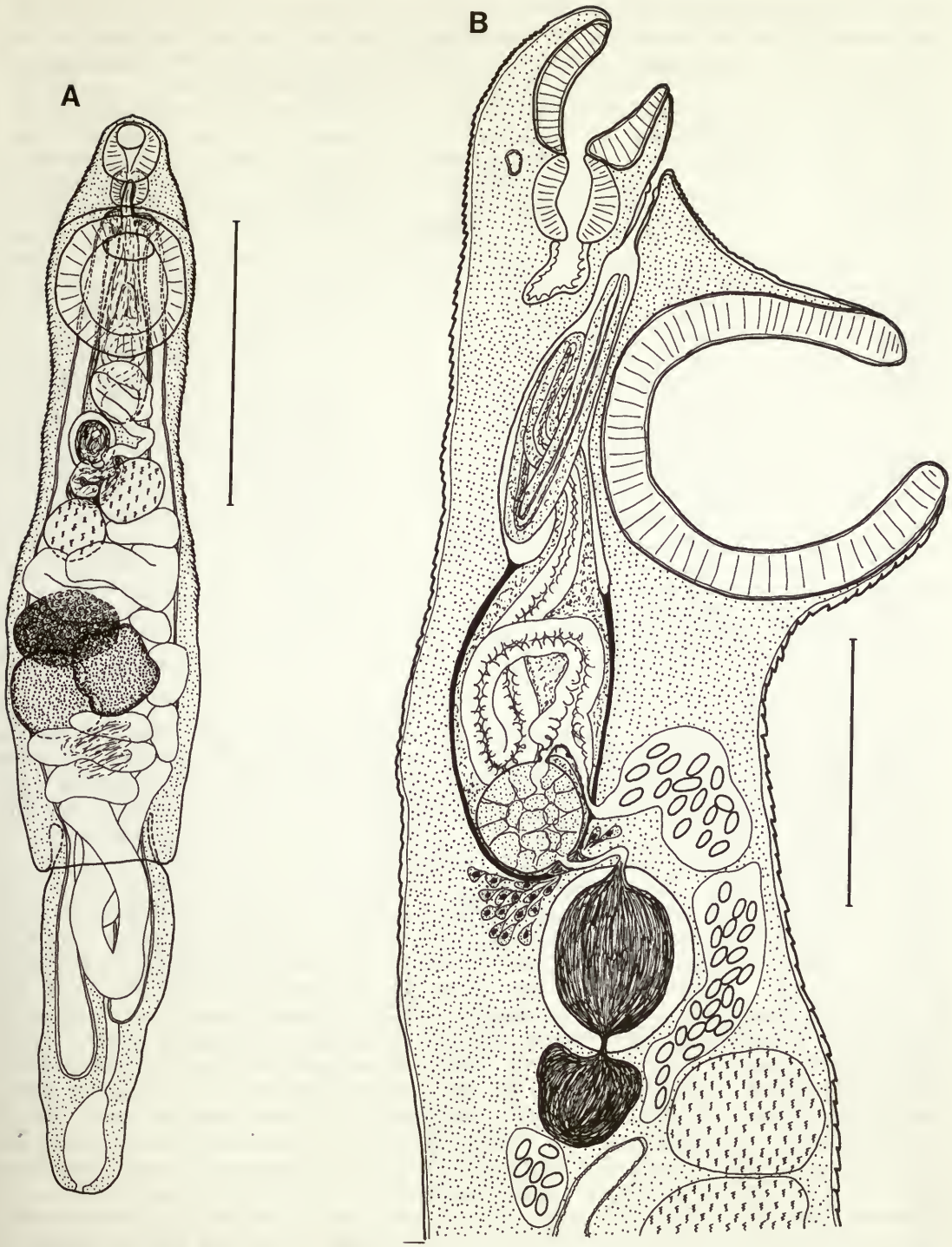


Fig. 11 *Glomericirrus macrouri.* (A) Entire worm, ex *Trachyrincus trachyrincus*; (B) Sagittal section of anterior half of worm, ex *Coryphaenoides rupestris.* Scale bars: A 500 μm; B 200 μm.

Table 8 Measurements of *Glomericirrus macrouri*

Authority	Armstrong (1974)	Gaevskaja (1975)	Campbell & Munroe (1977)	Present material
Name used	Genus novum D, species nova	*Hemiurus macrouri*	*Glomericirrus ulmeri*	*Glomericirrus macrouri*
Host	Macrourids	*Coryphaenoides rupestris*	*Coryphaenoides* spp.	*Coryphaenoides rupestris* etc.
Locality	Gulf of Mexico, Caribbean	North Mid-Atlantic Ridge	Hudson Canyon, NW Atlantic	NE Atlantic
Length (mm)	1·9–2·9	2·79	1·7–3·1	1·35–2·15
Breadth (mm)	0·6–0·87	0·68	0·39–0·6	0·22–0·42
Ecsoma (mm)	0·42–0·89	1·43	0·45–0·82	0–0·82
Forebody (mm)	0·2–0·43	–	–	0·12–0·21
Oral sucker (mm)	0·08–0·12 × 0·09–0·12	0·1 × 0·12	0·1–0·13 × 0·09–0·12	0·09–0·12 × 0·09–0·11
Ventral sucker (mm)	0·21–0·31 × 0·23–0·26	0·31 × 0·35	0·25–0·35 × 0·23–0·25	0·2–0·31 × 0·21–0·3
Sucker-ratio	1 : 2·05–2·54	1 : 3	1 : 2·2–3·1	1 : 2·2–2·57
Testes (mm)	0·06–0·22 × 0·15–0·27	0·09–0·2 × 0·15–0·23	0·11–0·27 × 0·07–0·18	0·05–0·13 × 0·07–0·18
Ovary (mm)	0·12–0·21 × 0·18–0·28	0·15 × 0·26	0·08–0·21 × 0·15–0·3	0·08–0·14 × 0·09–0·19
Vitelline masses (mm)	0·11–0·22 × 0·14–0·23	0·2 × 0·15–0·26	0·12–0·31 × 0·11–0·23	0·12–0·16 × 0·12–0·21
Eggs (μm)	21–27 × 13–16	23 × 14	19–24 × 12–14	22–26 × 11–14

the two parts is surrounded by a sphincter. The seminal vesicle occurs between the testes and the ventral sucker, but is usually closer to the testes, and often extends dorsally or dorso-laterally to the anterior testis. Anteriorly the muscular, distal part gives rise to a narrow, aglandular duct, which may be convoluted or straight, depending upon how close the seminal vesicle is to the base of the sinus-sac. In our sectioned material the duct is relatively short and convoluted. It leads to the base of the sinus-sac and passes through the wall of this organ. In our sectioned material there is no clear evidence, such as the nature of the lining of the duct, which indicates that it is or becomes the pars prostatica (cf. Campbell & Munroe, 1977). There are a number of external prostatic gland-cells, but they appear to surround only the distal end of this duct (Fig. 11B). As it passes through the wall of the sinus-sac, the wall of the duct appears to become wider and more glandular: this very short region may well be the pars prostatica (*sensu stricto*). Within the *sinus-sac* this opens into a very distinct glandular ejaculatory vesicle (terminology of Gibson & Bray, 1979). In our sections there is no evidence that the external prostatic cells surrounding the base of the sinus-sac pass through the wall of the sinus-sac and open into this organ. It seems likely, therefore, that the pars prostatica is a very reduced structure, as it is in several of the lecithochiriines where a glandular ejaculatory vesicle occurs. The lumen of the ejaculatory vesicle is almost filled with large, anucleate cells or blebs typical of the glandular form of this organ. The sinus-sac itself is large, oval and sunk deep within the body. It is usually situated in the anterior hindbody or postero-dorsally to the ventral sucker; but, although this was not seen in our material, it may apparently occur antero-dorsally to this sucker, its position depending upon the state of eversion of the sinus-organ, the state of contraction of the body and the amount of pressure applied to the specimen during fixation and mounting. The terminal portion of the uterus enters the base of the sinus-sac just antero-ventrally to the male duct and passes over the ventral surface of the ejaculatory vesicle (Fig. 11B). It widens as it passes anteriorly and the ejaculatory vesicle opens into it distally via a sphincter to form an hermaphroditic duct. This is

usually a very convoluted structure, but the amount of convolution is reduced when the sinus-organ is greatly everted. Dorsally to the ventral sucker or slightly anterior or posteriorly to this, depending upon its position, the sinus-sac joins the very deep genital atrium. The latter may be cylindrical or taper anteriorly, depending upon the amount of convolution of the sinus-organ. At the junction of the sinus-sac and the genital atrium the hermaphroditic duct passes into a large, permanent, relatively amuscular and often convoluted sinus-organ. This organ may end within the genital atrium or protrude through the genital pore (in specimens of *G. thoria* we have seen it protrude up to one-third the length of the body). The genital pore occurs mid-ventrally, roughly at the level of the junction between the oral sucker and the pharynx. In several of the specimens, including the sectioned material, the distal portion of the genital atrium, roughly equivalent in length to the pharynx, is slightly narrower and has a thicker lining and a more muscular wall: when withdrawn the sinus-organ usually terminates immediately behind this region (Fig. 11B).

The transversely oval *ovary* occurs subventrally on either side of the worm within about the middle third of the hindbody, although in extremely extended or contracted forms it may be posterior or anterior to this region, respectively. The oviduct leaves the ovary posteriorly and receives the duct from Juel's organ. It then continues postero-laterally over the lateral surface of Mehlis' gland, and, immediately prior to entering Mehlis' gland postero-laterally, it receives the vitelline ducts, apparently together. Within Mehlis' gland the oviduct swells slightly to form what is probably the oötype and then passes anteriorly. Mehlis' gland is situated posteriorly to the ovary and antero-dorsally to the vitellarium. Juel's organ is large and situated dorsally or antero-dorsally to Mehlis' gland. The *uterus* leaves Mehlis' gland anteriorly and immediately loops back over the dorsal surface of this organ, its initial loops being surrounded by small gland-cells. Posterior to Mehlis' gland it widens to form a uterine seminal receptacle. The latter is often a very large structure with spermatozoa filling much of the uterus posterior to the vitellarium. The uterine coils descend on the ovarian side of the body, usually reaching into the ecsoma, although not normally as far as the caeca. They then ascend on the opposite side of the body. The distribution of the uterus anteriorly to the ovary is variable, depending upon the displacement of the testes and the seminal vesicle; but usually, at the level of the anterior margin of the ovary, the uterus extends across the body ventrally and normally fills the space between the ovary and the posterior testis (Fig. 11A). It then passes dorsally to the testes, occasionally looping ventrally to the posterior testis, and then coils ventrally or ventro-laterally to the seminal vesicle, prior to passing dorsally and narrowing considerably to enter the base of the sinus-sac. There is no obvious delineation of a metraterm. The uterus contains numerous small, operculate eggs. The *vitellarium* is composed of two indistinctly lobed masses, which occur slightly obliquely immediately posterior to the ovary, the anterior of the two masses being more medially positioned and the other being more directly posterior to the ovary. If lobation is distinguishable on masses, then it normally occurs as four lobes on one mass and three on the other. The lateral collecting ducts leave the masses dorso-medially and appear to unite as they join the oviduct. In our sections there is no obvious common duct.

Discussion. The genus *Glomericirrus* was erected by Yamaguti (1937) for a new species, *G. amadai*, a single specimen of which he found in the stomach of the branchiostegid fish *Branchiostegus japonicus* off Japan. He later (1938) redescribed this species from further specimens recorded from *B. japonicus, Argentina kagoshimae, Cepola schlegeli* and *Lotella phycis*. We have examined the holotype, and, although it is very darkly stained and heavily flattened, we consider it to be very similar to our material from macrourids in the NE Atlantic, differing significantly only in the sucker-ratio (see Table 8), which is less than 1 : 2. More recent records of *G. amadai* by Machida *et al.* (1970) and Ichihara (1974) from *Aulopus japonicus* and *Percanthias japonicus* off the Tsushima Isles, Sea of Japan, by Korotaeva (1970) from *Nemadactylus valenciennes* and by Korotaeva (1982) from *Cyttoidops mccullochi*, both from Australian waters, do not include descriptions. It is, however, worth noting that we have been informed by Dr Ichihara (*in litt.*) that his specimens had a sucker-ratio of 1 : 2·2. It is clear that further work must be carried out on Japanese material; but, at present, the significant host and geographical disparity makes it more prudent to consider our material distinct from *G. amadai*.

G. propositus was originally described from two specimens taken from the macrourid *Coryphaenoides garmani* off Japan by Yamaguti (1938). There appears to be no further records of this name in the literature. We have examined Yamaguti's holotype and consider that it is very similar to the present material from macrourids of the north-east Atlantic, except for a marginal difference in egg-size and the position of the sinus-sac. Yamaguti gives the egg-length as being 24–33 μm, but we made the range in eggs from the distal region of the uterus in the holotype to be 24–29 μm, with the majority being about 26–27 μm, and thus marginally larger than in forms from the Atlantic (see Table 8). With regard to the position of the sinus-sac, a close examination of the type-specimen clearly shows that it has been heavily flattened and the alignment of the crenulate plications suggests that the ventral sucker has been pushed back during the flattening process. Thus the sinus-sac could have been forced forward. Although the sinus-sac is postero-dorsal or posterior to the ventral sucker in our acetic-acid-fixed material, Armstrong (1974) noted its position as 'dorsal to acetabulum (occasionally antero-dorsal, rarely postero-dorsal to acetabulum)'. Furthermore, we have some poorly fixed material of *Glomericirrus* (see below) from *Arnoglossus* sp. (probably from the Gulf of Guinea) in which the sinus-sac ranges from antero-dorsal to posterior to the ventral sucker. The position of this organ is, therefore, probably variable, depending upon the contraction of the body, the contraction of the genital atrium, the method of fixation and the degree of flattening during fixation. However, because (1) we cannot be certain the position of the sinus-sac in Yamaguti's material is not normal, and because of (2) the slight difference in egg-size and (3) the geographical separation between these forms, we have refrained from calling our specimens *G. propositus*. Nevertheless, it is possible that further material from Japanese waters may prove the two forms to be conspecific.

In 1966 Nikolaeva described *Dinosoma thoria* from a single specimen taken from *Arnoglossus thori* in the Aegean Sea (although this species of fish is not supposed to extend as far east as the Aegean: Hureau & Monod, 1973; Wheeler, 1978). We agree with Toman (1973), who suggested that this species rightfully belongs to *Glomericirrus*. The specimens mentioned above from *Arnoglossus* sp. probably from the Gulf of Guinea (the exact locality data have been lost) appear to be specimens of *G. thoria* n. comb. Furthermore, we could find no distinct morphological difference between these specimens and those from macrourids in the NE Atlantic, although the former specimens are not in as good a state of preservation as the latter. For the present we have retained *G. thoria* as a species distinct from the form from macrourids mainly because it is difficult to rationalize the totally different habitats of the two host-groups, one form occurring in coastal flatfishes and the other in bathyal macrourids (and a trachichthyid). The question of the synonymy of *G. thoria* and the species from macrourids can only be solved by the examination of well-preserved specimens from *Arnoglossus* and by an understanding of the life-history of these worms.

The first named material which we can be reasonably certain is identical to our material from macrourids is that described by Gaevskaja (1975) as *Hemiurus macrouri* from *Coryphaenoides rupestris* on the northern part of the Northern Mid-Atlantic Ridge. Gaevskaja (1978 *in litt.*) agreed with us that this was in fact a species of *Glomericirrus*, and she later (1979) transferred it to this genus and listed *G. ulmeri* Campbell & Munroe, 1977, as a synonym. The latter species, originally mentioned by Haedrich & Polloni (1976) as '*Glomericirrus* n. sp.', was recorded from *Coryphaenoides carapinus, C. leptolepis* and *C. armatus* from the Hudson Submarine Canyon on the edge of the continental shelf on the western side of the northern North Atlantic. Campbell *et al.* (1980) added *C. rupestris* to the list of hosts from the same region. Specimens from the western side of the North Atlantic had in fact been described earlier as 'Genus novum D, species nova' by Armstrong (1974), who recorded them from six species of the macrourid genera *Coelorhynchus, Hymenocephalus, Ventrifossa* and *Nezumia* in the eastern Gulf of Mexico off Florida (depth 364–728 m) and in the Caribbean Sea off Panama (depth 591 m). It had also been found in the NW North Atlantic by Zubchenko (1976; as *Hemiurus macrouri*; 1981*a,b*) in *Coryphaenoides rupestris* and *Nezumia bairdi*. We agree with Gaevskaja (1979), Campbell (1983), Gaevskaja & Aleshkina (1983) and Gaevskaja & Rodjuk (1983) that *G. ulmeri* is a synonym of *G. macrouri*. In conclusion, therefore, we have used the name *G. macrouri* for our material and note that *Trachyrincus trachyrincus* and *Hoplostethus atlanticus* are new host-records.

The following points are also worth noting. (1) Due to the fact that the tegumental plications of *Glomericirrus* spp. are crenulate, there has been confusion between this genus and *Dinosoma* Manter, 1934 (e.g. Nikolaeva, 1966). It is possible, therefore, that this may also be the case with *Dinosoma* sp. from the trachichthyid *Gephyroberyx japonicus* which Ichihara *et al.* (1965) reported off Japan, although as shown below, *Dinosoma* can occur in bathyal fishes. (2) As indicated by Manter (1970), *Glomericirrus septemlobus* Freitas & Kohn, 1965, is a lecithochiriine and probably a synonym of *Lecithochirium microstomum* Chandler, 1935. (3) Despite the fact that Szuks (1980) examined large numbers of *Coryphaenoides rupestris* in the Labrador Sea, surprisingly he did not record *G. macrouri:* he did, however, claim to have found the warm-water species *Parahemiurus merus* (see p. 38)! (4) We have elucidated, for the first time (Fig. 11B), exactly where the sinus-sac and the genital atrium unite and can thus present a much more accurate picture of the shape of the sinus-sac and the functioning of the terminal genitalia of this subfamily.

Subfamily **LECITHOCHIRIINAE** Lühe, 1901

Sterrhurinae Looss, 1907.
Brachyphallinae Skrjabin & Guschanskaja, 1955.
Tricotyledoniinae Skrjabin & Guschanskaja, 1955.
Trithelaminae Yeh, 1955.
Dissosaccinae Yamaguti, 1958.

DIAGNOSTIC FEATURES. Ecsoma usually well developed, occasionally reduced. Body-surface usually smooth, but occasionally plicated or rugate. Muscular 'shoulder-pads' present or absent. Presomatic pit and ventro-cervical groove present or absent. Testes tandem to symmetrical, usually oblique. Seminal vesicle elongate; constricted into two portions, which are occasionally separated by a duct, or tubular and convoluted; in bipartite forms anterior half may have thicker wall; normally in forebody, but forms with halves separated by duct may extend into hindbody. Pars prostatica short; vesicular or tubular; may extend slightly into base of sinus-sac; linked to seminal vesicle by short, aglandular duct. Sinus-sac present; rarely of 'open'-type; enclosing distinct ejaculatory (prostatic) vesicle and metraterm (or part of metraterm). Permanent sinus-organ absent. Genital atrium usually small or absent, occasionally well developed. Uterus mainly pre-ovarian or roughly equally distributed in pre- and post-ovarian fields. Eggs without filaments. Vitellarium seven digitiform to oval lobes in lateral groups of three and four, or with tendency to become two distinct lateral masses which often exhibit three and four lobes. Excretory arms united in forebody. Normally parasitic in gut or body-cavity of marine teleosts.

Key to the lecithochiriine genera occurring in the north-east Atlantic

1 Vitellarium seven distinct oval to digitiform lobes which may occur as two 3- and 4-lobed masses; body surface smooth . . . . . *Lecithochirium* (p. 61)
– Vitellarium two entire masses which may be indistinctly 3- and 4-lobed; body surface with plications . . . . . *Brachyphallus* (p. 90)

Genus *LECITHOCHIRIUM* Lühe, 1901

Sterrhurus Looss, 1907.
Ceratotrema Jones, 1933.
Jajonetta Jones, 1933.
Separogermiductus Skrjabin & Guschanskaja, 1955.
Magniscyphus Reid, Coil & Kuntz, 1965.
Neohysterolecitha Ahmad, 1977.

DIAGNOSTIC FEATURES. Ecsoma well or poorly developed. Body-surface smooth. Pre-oral lobe rarely with two lateral knobs ('horns'). Presomatic pit and/or ventro-cervical groove often present. Seminal vesicle bipartite, apparently tripartite or occasionally coiled; in forebody. Pars prostatica tubular, with wide lumen, to vesicular. Short, narrow extension of pars prostatica

and/or ejaculatory duct may be present within sinus-sac. Ejaculatory (prostatic) vesicle linked posteriorly to antero-dorsally with pars prostatica or ejaculatory duct. Temporary sinus-organ may form. Vitellarium two lateral masses; usually divided into three and four oval to digitiform lobes. Parasitic in gut (mainly stomach) or body-cavity of marine teleosts; also recorded from hepatic ducts and gills of marine teleosts and (?) gut of freshwater reptiles.

TYPE-SPECIES. *Lecithochirium rufoviride* (Rudolphi, 1819) [by original designation].

COMMENT. The systematics of this genus was discussed by Gibson & Bray (1979).

Key to the species of *Lecithochirium* recorded from the north-east Atlantic

1 Oral sucker with postero-lateral thickenings of wall which protrude into lumen of sucker . . 2
– Oral sucker without postero-lateral thickenings of wall 3
2 Two symmetrical, lateral projections ('horns') present on pre-oral lobe; parasitic in body-cavity of rockling or occasionally stomach of eels . . . . . *L. furcolabiatum* (p. 69)
– No projections present on pre-oral lobe; normally parasitic in stomach of eels . . . . . *L. rufoviride* (p. 62)
3 Vitellarium with seven digitiform lobes often arranged in rosette; normally parasitic in stomach of conger eels . . . . . *L. fusiforme* (p. 76)
– Vitellarium composed of two 3- and 4-lobed masses; parasitic in stomach of wide range of teleosts and body-cavity of rock-pool fishes, especially gobiids . . *L. musculus* (p. 83)

Lecithochirium rufoviride (Rudolphi, 1819) Lühe, 1901

Distoma rufoviride Rudolphi, 1819.
Distoma (Apoblema) rufoviride (Rudolphi) Dujardin, 1845.
Apoblema rufoviride (Rudolphi) Juel, 1889.
Hemiurus rufoviridis (Rudolphi) Looss, 1899.
(?) *Distoma grandiporum* Rudolphi of Olsson (1876).
(?) *Cercaria vaullegeardi* Pelseneer, 1906.
Distomum ocreatum Molin of Johnstone (1907).
Lecithochirium gravidum Looss, 1907.
Dissosaccus gravidus (Looss) Skrjabin & Guschanskaja, 1955.

TYPE-HOST AND LOCALITY. *Conger conger*, Naples, Italy.

RECORDS

(i) Material studied
(a) From the NE Atlantic

From the gut

Anguilla anguilla [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1984.9.19.1–12.
Conger conger [stomach] Moray Firth, Scotland (58°N, 02°W; depth 188 m, 152–186 m and 160–192 m; Sept., 1976). BM(NH) 1984.9.19.13–82.
—— [?] Locality unknown. BM(NH) 84.9.20.4–12.
—— [stomach] Plymouth, Devon, England. (May) BM(NH) 1932.11.29.11–21 (Material of Baylis & Jones, 1933; 631; Baylis, 1939: 478); material collected by M. Rothschild – BM(NH) 1932.11.22.56; material collected by J. S. Steward – BM(NH) 1938.11.4.228–240; (May, 1972) BM(NH) 1984.9.19.83–87.
—— [?] Guernsey, Channel Islands. Collected by R. H. Le Pelley. BM(NH) 1924.3.15.33–52.
—— [stomach] Irish Sea. Collected by F. G. Rees. BM(NH) 1976.4.9.114.
—— [?] Langesund, Norway (Jan., 1888). Zoological Museum Oslo Reg. No. C. 60.
—— [stomach] Barra Bank, off W Scotland (57°N, 09°W; depth 450 m; Oct., 1978). BM(NH) 1984.9.19.88.
—— [gut] Locality unknown. Collection of J. Mahon. BM(NH) 1980.7.25.40–41.
—— [stomach] N. of Scotland (59°N, 02°W; depth 79 m; May, 1984). BM(NH) 1984.9.19.89.
Lophius piscatorius [stomach] Plymouth, Devon, England. Collected by M. Rothschild. BM(NH) 1932.11.22.53–55.
(?) *Molva molva* [stomach] Kristineberg, Sweden (Aug., 1976). BM(NH) 1984.9.19.90.

Encapsulated on viscera

(?) Gadus morhua [pyloric caeca] Faeroes. Collected by M. Køie. BM(NH) 1984.9.19.91.

(b) From elsewhere
None.

(ii) NE Atlantic records from the literature

From the gut

Anguilla anguilla [stomach] Varberg, Sweden (July). Olsson (1868: 49; as *Distoma rufoviride*).
—— [stomach and branchial cavity] Bergen, Norway. (Aug.) Olsson (1868: 49; as *D. rufoviride*). [?] (July, Aug.) Lönnberg (1890: 44; as *D. rufoviride*).
—— [stomach] Grafverna and Näset, Bahusiae (Bohuslän), Sweden (July–Sept.). Olsson (1876: 20; as *D. rufoviride*).
—— [?] Kristineberg, Sweden. (Summer, 1889) Juel (1889: 8; as *Apoblema rufoviride*); Lönnberg (1889: 62; as *D. rufoviride*); Looss (1908: 149; as *Lecithochirium gravidum*).
—— [stomach] St. Andrews, Scotland. Nicoll (1907: 72).
—— [stomach] Plymouth, Devon, England. Nicoll (1914: 485).
—— [stomach] Milford Haven, Dyfed, Wales. Mhaisen (1977; 1983: 345; as *L. gravidum*).
Conger conger [stomach] (Rennes), Brittany, France. Dujardin (1845: 421: as *D. rufoviride*: see Dollfus, 1968: 145).
—— [stomach] Ireland. Bellingham (1844: 425; as *D. rufoviride*).
—— [mouth, stomach] Belgium. van Beneden (1871: 82; as *D. rufoviride*).
—— [stomach, intestine] Øresund, Sweden (March). Olsson (1876: 20; as *D. rufoviride* and (?) *D. grandiporum*).
—— [stomach] Irish Sea. Herdman (1904: 39; as *Distomum rufoviride*); Johnstone (1907: 277; as *D. ocreatum*; see Bruce *et al.*, 1963: 76); Rees & Llewellyn (1941: 391, 393).
—— [stomach] Millport, Firth of Clyde, Scotland. Elmhirst & Martin (1910: 477); Nicoll (1910: 349, 357); D. O. Jones (1943: 47).
—— [stomach] Aberdeen, Scotland (Sept., 1908). Nicoll (1913: 193).
—— [stomach] Plymouth, Devon, England. Nicoll (1914: 485); Baylis & Jones (1933: 631); Baylis (1939: 478); Dawes (1947: 287); Bray (1973: 178); (Sept., Nov.) Matthews (1982*b*: 24).
—— [stomach] Guernsey, Channel Isles (July). Baylis (1928: 332); Bray (1973: 178).
—— [stomach] Galway, Eire. Little (1929: 25).
—— [stomach] Roscoff, Finistère, France (June, 1937). Sproston (1939: 45, 50).
—— [stomach] Irish Atlantic Slope (54°N, 12°W; depth 220–275 m; Aug., 1939). Rees & Llewellyn (1941: 391, 393).
—— [stomach] Milford Haven, Dyfed, Wales. D. O. Jones (1943: 47).
—— [?] Albufeira, Algarve coast, Portugal (Aug., 1954). Tendeiro & Valdez (1955*b*: 100).
—— [?] Sines, Baixo Alentejo coast, Portugal. Tendeiro & Valdez (1955*b*: 100).
—— [?] North Sea off Netherlands. Willemse (1968: 85).
Lophius piscatorius [stomach] Plymouth, Devon, England. Nicoll (1914: 485); Baylis & Jones (1933: 631); Baylis (1939: 478); Dawes (1947: 287); (June) Matthews (1982*b*; appendix).
—— [?] NE Atlantic. Gaevskaja (1978*a*: 83; possibly not an original record).
(?) *Osmerus eperlanus* [intestine] Belgium. van Beneden (1871: 70; as *Distoma rufoviride*).
(?) *Scophthalmus rhombus* [stomach, intestine] Belgium. van Beneden (1871: 74; as *D. rufoviride*).
(?) *Zoarces viviparus* [mouth] Belgium. van Beneden (1871: 49; as *D. rufoviride*).

Encapsulated on viscera

Those records close to the SW British Isles must be treated as questionable, as some could be *L. furcolabiatum* (see also *L. furcolabiatum* and *Synaptobothrium caudiporum* for other questionable records, some of which might be *L. rufoviride*).
(?) *Blennius pholis* [intestine, viscera] Roscoff, Finistère, France (June, 1937). Sproston (1939: 40; as *L. gravidum*).
—— [liver, occasionally free in gut] Aberystwyth and Milford Haven, Wales. Mhaisen, in Popiel (1978: 155; as *L. gravidum*); Mhaisen (1977 and 1983: 345; as *L. gravidum*).
(?) *Psetta maxima* [visceral cavity] Fish from North Wales reared at Moidart, Scotland. DAFS (1974: 40).

Aspects of biology. The full life-history of this species is not known. Chabaud & Campana-Rouget (1959) discovered some immature specimens of a lecithochiriine encapsulated in gobiid, labrid and blenniid teleosts in an aquarium at Banyuls-sur-Mer on the Mediterranean coast of France. In the same aquarium they found a cystophorous cercaria in the top-shell *Gibbula varia*, which they thought to be identical with *Cercaria vaullegeardi* Pelseneer, 1906. This is an unusual cystophorous cercaria in that it apparently arises from a daughter-sporocyst rather than a redia,

which is the normal occurrence in hemiuroids. Nevertheless, according to Matthews (1980), this type of daughter-sporocyst is a modified redia, as the birth-pore and birth-canal of the former are homologous with the mouth, pharynx and caecum of the latter. Although Chabaud & Campana-Rouget failed to find copepods infested with the metacercariae, they assumed that these cercariae were the larval form of the encapsulated, immature forms from fishes. Knowing that *L. fusiforme* occurred locally in *Conger conger*, they assumed that these encapsulated forms were immature specimens of the latter species, and thus formed the missing link between the metacercariae in copepods and the adults in congers. Unfortunately, there was no direct evidence for this relationship, and, considering both the sucker-ratio in the figure of Chabaud & Campana-Rouget (1959) and the work of Carrère (1938), these encysted forms are perhaps more likely to have been *L. rufoviride*. The records of *Cercaria vaullegeardi* from our region are given on p. 000, although it is likely that there has been some confusion between the larval forms of different species, as there are small differences between the descriptions. It does seem likely, however, that some of the records of *C. vaullegeardi* refer to the larval stage of *L. rufoviride*, although we have biochemical data (see Gibson, Rollinson & Matthews, 1985) which indicate that *C. vaullegeardi* of Matthews (1980, 1981*a*,*b*, 1982*b*) is *L. furcolabiatum*.

Similarly, the records of encapsulated forms, which may be progenetic, from the viscera of various fishes, such as gobiids and labrids, may also refer to a mixture of species, although it seems likely that many are *L. rufoviride*. In the region of the SW British Isles, however, many of the records, especially those from rock-pool fishes, are *L. furcolabiatum*. Similar young, usually immature, worms may be found in the stomach or intestine of a wide variety of teleosts; but these are, presumably, either accidental infestations which have been recently ingested or specimens *en route* to the body-cavity and re-encapsulation.

Other work on this topic includes the early comments of Looss (1908), who mentioned that the young form of '*L. gravidum*' occurs encapsulated in labrids, *Syngnathus acus*, *Hippocampus ramulosus* and other fishes at Trieste, and Carrère (1938), who claimed to have fed some encapsulated specimens from *Gobius niger* to the frog *Hyla arborea* and to have recovered worms in good condition with some development of the gonads after three days. Carrère also infested specimens of *Pomatoschistus minutus* with cysts from *Symphodus cinereus* and obtained ovigerous worms. These results are, however, questionable, for, as mentioned above, the encapsulated worms are often ovigerous.

The normal definitive host of this species is *Conger conger*; but, especially in the northern part of its range where congers are less common, it also occurs commonly in *Anguilla anguilla*. It has also been recorded at Plymouth in the stomach of *Lophius piscatorius*. We have examined three specimens collected from this host at Plymouth and can confirm that they are relatively large and ovigerous, although perhaps containing fewer eggs than similar sized specimens from congers. Although it is possible that *L. rufoviride* might survive in *L. piscatorius*, this is not certain, as specimens could be acquired accidentally if this fish preys upon eels or small fishes harbouring progenetic encapsulated worms.

In summary, therefore, the life-history appears to be as follows: (1) mother-sporocyst and daughter-parthenitae (producing (?) *Cercaria vaullegeardi*) in *Gibbula*; (2) metacercariae in copepods; (3) small, encapsulated, immature (but occasionally ovigerous) forms on viscera of small planktivorous fishes; and (4) mature adults in eels.

The distribution of this species appears to be Lusitanean, probably mimicking its major definitive host, *C. conger*, as it occurs in the Mediterranean Sea and the eastern coast of the North Atlantic between the Canaries and Bergen, Norway (we have recorded an encapsulated specimen, probably of this species, off the Faeroes). The absence of *C. conger* in the Black Sea presumably explains the absence of definitive records of this species from that region. It is worth noting that Sey (1970) reported this species from another congrid, *Ariosoma balearicum*, in the Adriatic Sea.

PREVIOUS DESCRIPTIONS. Dujardin (1845: 421; as *Distoma rufoviride*; brief); Wagener (1860: 178; as *D. rufoviride*; figured); Olsson (1868: 49; as *D. rufoviride*; brief); Juel (1889: 6; as *Apoblema rufoviride*; terminal genitalia); Johnstone (1907: 277; as *Distomum ocreatum*); Looss (1908: 144; as

L. rufoviride and *L. gravidum*; detailed); Timon-David (1937: 19; as *L. rufoviride* and *L. gravidum*; brief); D.O. Jones (1943: 47; detailed); Dawes (1947: 287); Janiszewska (1953: 29).

DESCRIPTION (Figs 12, 13, 16A,B, 17F). This description is based upon 40 whole-mounted and four sectioned specimens from *Conger conger* and *Anguilla anguilla*. The body of this worm is fusiform, its breadth depending upon the state of contraction. Flattened specimens may be up to twice the size of similar unflattened worms and vary in shape from fusiform to oval. Although generally quite large for a hemiruid, there is often a relatively wide range of sizes found: see Table 9 for the measurements of this species. The *ecsoma* in preserved specimens is usually, but not always, withdrawn, although it often protrudes slightly in flattened material. The body surface is smooth. The large *oral sucker* is ventrally subterminal, being surmounted by a distinct pre-oral lobe which may be squared off. A regular arrangement of papillae occur surrounding the oral sucker (Fig. 16A,B), but these are usually difficult to discern. Within the postero-lateral regions of the wall of the oral sucker are two distinct, symmetrical thickenings which protrude into the lumen (Figs 12, 13, 16A,B). A less obvious thickening also occurs in the anterior wall of this sucker. The spherical *ventral sucker* is slightly larger than the oral sucker, the ratio usually being in the region of 1 : 1·2–1·6, and is situated at about one-third of the body-length from the anterior end. A small presomatic pit is present between the genital pore and the anterior margin of the ventral sucker (Fig. 13B,E), but this is often difficult to see in whole-mounts.

There is no prepharynx, but a small (in relation to the size of the oral sucker) *pharynx* gives rise to a distinct, short and sac-like oesophagus. The oesophagus opens posteriorly, postero-dorsally or dorsally, depending upon the state of contraction, via a sphincter into a short commissure which extends between the two gut-caeca. The commissure almost immediately dilates laterally on each side to form a distinct 'Drüsenmagen'. From these the caeca extend laterally, antero-laterally or postero-laterally and then curve to run posteriorly in the lateral or dorso-lateral fields. At about the 'shoulder-region' the caeca normally become much wider than they were initially. They end blindly close to the proximal end of the ecsoma or occasionally inside the proximal end of this organ when it is extruded.

The excretory pore occurs terminally on the ecsoma. It leads into the stout stem of a tubular, Y-shaped *excretory vesicle*, which passes forward medially and bifurcates at about the level of the testes. The two narrow arms pass into the forebody laterally and unite dorsally to the oral sucker.

The two oval *testes* occur ventro-laterally and symmetrically or slightly obliquely close to the posterior margin of the ventral sucker. They are normally widely separated. The two vasa efferentia unite as they meet the thin wall of the proximal end of the seminal vesicle. The latter organ is essentially bipartite, but often appears to be tripartite (Fig. 13B). Its proximal part is large, but variable in size, elongate-saccular and is often curved, folded or constricted such that it appears to be divided with a small, distinct distal region. The distal part of the seminal vesicle is smaller than the proximal part and possesses a thicker and more muscular wall. It is flask-shaped and opens via a short, tapering duct into the pars prostatica. Surrounding and closely applied to the surface of this duct and the distal part of the seminal vesicle is a layer of large, non-staining, granular cells (Fig. 13B,C). The seminal vesicle may be entirely in the posterior part of the forebody, but the large proximal part usually extends back in the medial or submedial field dorsally to the ventral sucker, occasionally reaching the posterior margin of this sucker. The pars prostatica (Fig. 13B,C) is short, wide, tubular, surrounded by a layer of gland-cells proximally, possesses a thick lining of anuclear blebs which almost fill the lumen, and usually extends into the base of the sinus-sac. It is not absolutely clear, but it appears that the ducts of the external gland-cells pass through the diffuse musculature of the proximal sinus-sac, although no sign of the ducts was seen inside the sinus-sac associated with the distal part of the pars prostatica. The *sinus-sac* is small, claviform and weakly muscled, especially proximally. It receives both the pars prostatica and the metraterm through wide openings at its base. The junction of the pars prostatica and the ejaculatory duct, which is often some way inside the base of the sinus-sac, is narrow; but the ejaculatory duct immediately opens out to form a distinct, but often small, ejaculatory vesicle (Fig. 13B,C). This vesicle has a smooth lining, i.e. there are no blebs present, although the blebs lining the pars prostatica usually do protrude through into the proximal

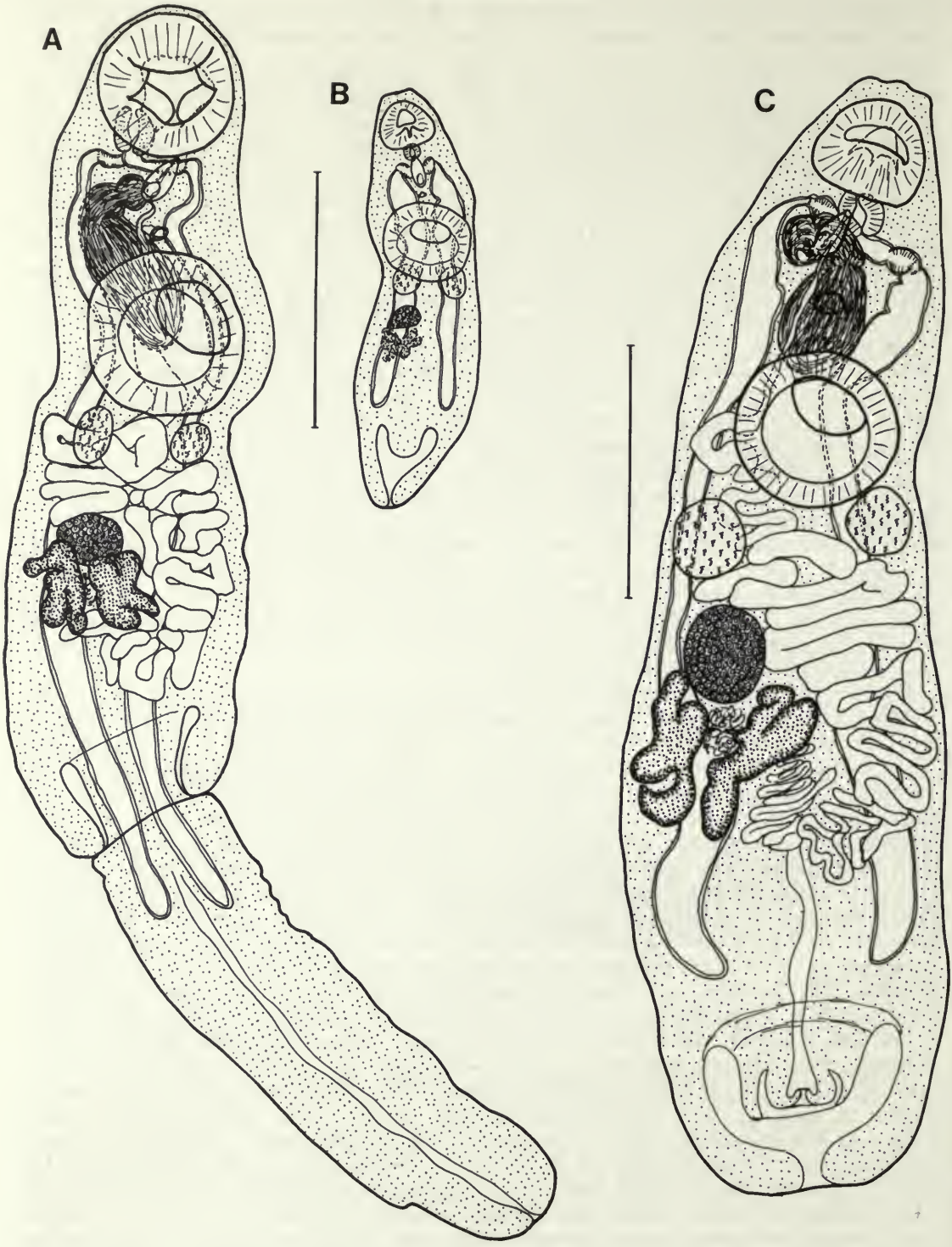


Fig. 12 *Lecithochirium rufoviride*. (A,B,C) Entire worms, ex *Conger conger*. Scale bars: 1 mm.

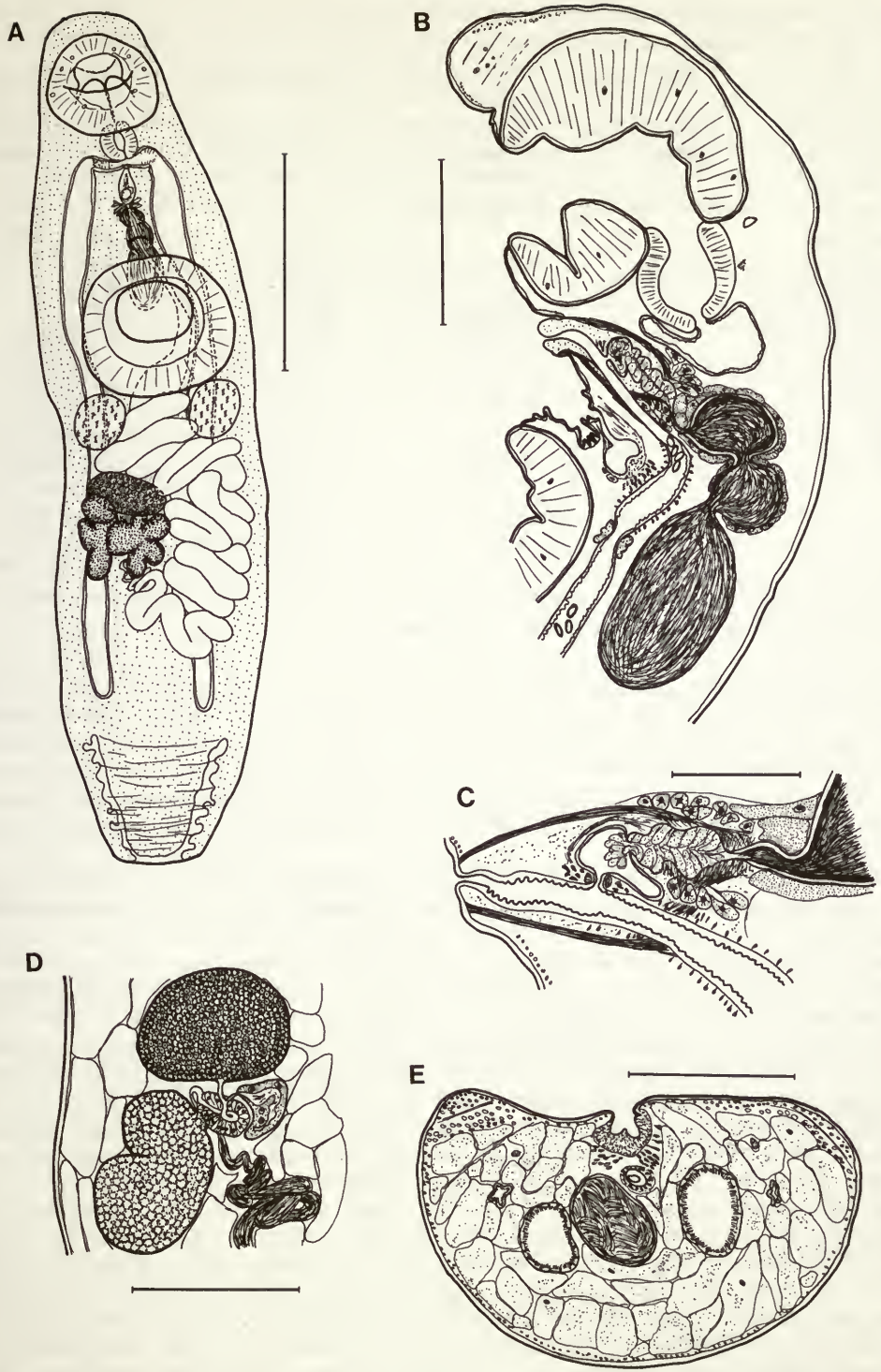


Fig. 13 *Lecithochirium rufoviride*. (A) Entire worm, ex *Anguilla anguilla,* Kristineberg; (B) Sagittal section of forebody, ex *Conger conger*; (C) Terminal genitalia, ex *A. anguilla*; (D) Ovarian complex, ex *A. anguilla;* (E) TS of forebody at level of presomatic pit, ex *C. conger*. Scale bars: A 1 mm; B,D,E 300 μm; C 100 μm.

Table 9 Measurements of *Lecithochirium rufoviride*

Authority	Looss (1908)	D. O. Jones (1943)	Present material	Present material
Host	*Conger conger*	*Conger conger*	*Conger conger*	*Anguilla anguilla*
Locality	Naples	Millport, Scotland	NE Atlantic	Kristineberg, Sweden
Length (mm)	3–7·5	4–6	0·97–8·2	1·96–3·9
Breadth (mm)	0·5–1·5	1·7	0·2–2·6*	0·55–1
Ecsoma (mm)	–	–	0–0·25	0–0·42
Forebody (mm)	–	1/3 length	0·35–2·2	0·5–1·2
Oral sucker (mm)	0·3–0·8 diam.	0·7 diam.	0·1–1·0 × 0·1–0·95	0·23–0·47 × 0·24–0·55
Ventral sucker (mm)	0·4–1 diam.	0·79 × 0·83	0·15–1·14 × 0·18–1·3	0·34–0·74 × 0·37–0·8
Sucker-ratio	–	1 : 1·14	1 : 1·21–1·7	1 : 1·25–1·54
Testes (mm)	–	0·33 × 0·29	0·03–0·35 × 0·04–0·45	0·12–0·23 × 0·12–0·24
Ovary (mm)	–	0·33 × 0·42	0·02–0·35 × 0·02–0·45	0·13–0·26 × 0·16–0·26
Eggs (μm)	22 × 13	18 × 9	17·5–24 × 10–13*	22–24 × 13–14

*Includes many flattened specimens, many with collapsed eggs.

region of the vesicle. Distally the vesicle unites ventrally with the metraterm to form the hermaphroditic duct, which appears to be a continuation of the metraterm. The hermaphroditic duct is short, stout and tubular. It opens terminally through the genital pore or is everted slightly in fixed specimens to form a small 'temporary sinus-organ' which protrudes through the genital pore. The genital atrium is either absent or very small. The genital pore is situated mid-ventrally in the forebody at about the level of posterior margin of the pharynx, but its exact position varies with the state of contraction.

The transversely oval *ovary* is situated ventro-laterally on either side of the body a short distance from one of the testes, although in mature specimens it is usually separated from this testis by coils of the uterus. The short oviduct arises from the posterior region of the ovary. It passes postero-medially and receives the duct from Juel's organ (Fig. 13D) and the common vitelline duct before entering a compact Mehlis' gland, which is situated immediately posterior and slightly medial to the ovary. Juel's organ is well developed, with the usual 'inner vesicle' and 'amoeboid' cells, but it is slightly arcuate, being closely associated with the antero-dorsal surface of Mehlis' gland. Juel's organ and Mehlis' gland appear to be bound together by a membranous covering; but a close examination suggests that this is probably just the walls of the neighbouring parenchymatous cells. After passing through Mehlis' gland the ovo-vitelline duct widens to form the *uterus*, the first part of which, coiled postero-dorsally to the ovarian complex, forms a uterine seminal receptacle. The uterus then winds back posteriorly, following a number of wide loops to about the level of the base of the ecsoma. It does not normally extend into the ecsoma. The uterus then winds anteriorly on the opposite side of the body to the ovarian complex; but at about the level of the ovary the loops extend into the dorsal field between the caeca and across the body ventrally between the ovary and the testis on the ovarian side of the body. At the level of the testes and the ventral sucker most of the uterine coils are intercaecal in the dorsal field; but, at the level of the anterior margin of the ventral sucker or just anterior to it, the uterus passes through a distinct sphincter to form a thick-walled, muscular metraterm (Fig. 13B), which is surrounded by small gland-cells. The metraterm passes directly forward ventrally or ventro-laterally to the seminal vesicle and enters the base of the sinus-sac, within which it unites with the ejaculatory vesicle to form the hermaphroditic duct. It should be noted that the course of the uterus may vary

somewhat and may be considerably altered by pressure or contraction during fixation. The uterus contains numerous small, operculate eggs. The *vitellarium* is composed of two lobed masses which lie side by side immediately posterior or postero-ventral to the ovary. The lobes, which normally number three on one mass and four on the other, are oval to digitiform, their length usually being within the range of one to three times the breadth. It is common for some of the lobes to be bifid, thus giving the impression that a greater number of lobes are present. The two masses give rise to two extremely short, stout vitelline ducts which pass dorso-medially and unite to form a similarly short, but narrow, common duct that opens into the oviduct. There is no vitelline reservoir.

Discussion. *Lecithochirium rufoviride* was originally described by Rudolphi (1819) from specimens from the stomach of *Conger conger* in the Mediterranean Sea. Since that time it has been recorded on many occasions from this host, often concurrently with *L. fusiforme*, and occasionally from *Anguilla anguilla*. *L. gravidum* was erected by Looss (1907, 1908) for specimens from *A. anguilla*, but he mentioned that it also occurred in *Psetta maxima, Gobius cobitis* (= *capito*) and *C. conger*. Although recognizing that it was very similar to *L. rufoviride*, he differentiated it on its smaller size and greater disparity in size of the two suckers. Our examination of specimens from *A. anguilla* at Kristineberg, Sweden, the same host and locality as some of Looss' material, indicates that, although the specimens from this host do tend to be smaller than those from *C. conger*, there appears to be no morphological reason for distinguishing the two forms at the specific level. The majority of records of *L. gravidum* from *C. conger* in the literature are in fact *L. fusiforme* (see p. 77). Skrjabin & Guschanskaja (1955*a*) placed *L. gravidum* in the genus *Dissosaccus* Manter, 1947, because they mistakenly believed that there was no ejaculatory (prostatic) vesicle present; but the presence of this structure is in fact one of the main morphological features which distinguishes the subfamily Lecithochiriinae. *Dissosaccus* can be distinguished from *Lecithochirium* by the fact that the two portions of its bipartite seminal vesicle are connected by a long, narrow duct (Gibson & Bray, 1979).

Lecithochirium furcolabiatum (Jones, 1933) Dawes, 1947*

Ceratotrema furcolabiata E. I. Jones, 1933.
Cercaria vaullegeardi Pelseneer of Matthews (1980, 1981*a*,*b*, 1982*b*).

Type-host and locality. *Ciliata mustela*, Wembury Bay, Plymouth, Devon, England.

Records

(i) Material studied
(a) From the NE Atlantic

From the gut

Anguilla anguilla [stomach] Rock-pools, St. Mary's, Scilly Isles (July, 1978). Collected by R. J. Knowles from two eels. BM(NH) 1984.9.19. 92–126.

Conger conger [stomach] Plymouth, Devon, England. Collected by J. S. Steward (single specimen amongst *L. rufoviride* BM(NH) 1938.1.4.228–240) BM(NH) 1984.9.19.127. Collected by B. F. Matthews (1984: several worms used by us for iso-electric focusing).

Free in body-cavity

Ciliata mustela [body-cavity] Rock-pools, Wembury Bay, Plymouth, Devon, England (Sept., 1932). Type-specimen of *Ceratotrema furcolabiata*. BM(NH) 1933.6.14.101. (Material of E. I. Jones, 1933: 248).
—— [body-cavity] Wembury Bay, Plymouth, Devon, England (June, July, 1978). Collected by B. F. Matthews. BM(NH) 1984.9.19.128–330.
—— [?] Slapton, Devon, England. Collection of J. Mahon. BM(NH) 1980.7.25.28–29.
—— [body-cavity] Carna, Galway Bay, Eire (1982). Collected by C. Cheetham. BM(NH) 1984.9.6.77–79.

*This combination was also made in 1947 by Manter; but his publication appeared in September, whereas, according to the official stamp, the BM(NH) copy of Dawes' book was received on 22 April 1947.

Encapsulated on viscera

Due to their proximity to records of *L. furcolabiatum* most of these are treated as questionable records of this species, although it is possible that some are *L. rufoviride*. In cases which are not questioned, evidence of the development of 'horns' was seen.

(?) *Blennius pholis* [body-cavity] Coast of Galway, Eire. Collected by M. O'Farrell. BM(NH) 1984.9.19. 331–332.

(?)—— [body-cavity] Coast of Co. Wexford, Eire. Collected by M. O'Farrell. BM(NH) 1984.9.19.333–334.

—— [on liver and intestine] Wembury Bay, Plymouth, Devon, England. (Oct., 1980) BM(NH) 1984.9.19. 335–336. [mesenteries] (June, 1978). Collected by B. F. Matthews. BM(NH) 1984.9.19.337–342.

(?) *Coryphoblennius galerita* [body-cavity] Coast of Galway, Eire. Collected by M. O'Farrell. BM(NH) 1984.9.19.343.

(?) *Gaidropsarus vulgaris* [around mesenteric vein] Wembury Bay, Plymouth, Devon, England. Collected by B. F. Matthews. BM(NH) 1984.9.19.345–352.

(?) *Gobius paganellus* [on viscera] Wembury Bay, Plymouth, Devon, England (June, 1978), collected by B. F. Matthews, BM(NH) 1984.9.19.353–354; Oct (1980), BM(NH) 1984.9.19.355–357.

(?) *Labrus bergylta* [on intestine] Wembury Bay, Plymouth, Devon, England (Oct., 1980). BM(NH) 1984.9.19.358.

(?) *Symphodus melops* [on intestine] Wembury Bay, Plymouth, Devon, England (Oct., 1980). BM(NH) 1984.9.19.344.

Taurulus bubalis [on viscera] Plymouth, Devon, England (Oct., 1980) BM(NH) 1984.9.19.359–360; Wembury Bay, Plymouth (June, July, 1978), collected by B. F. Matthews. BM(NH) 1984.9.19.361–367; [stomach] (Single specimen) Wembury Bay, Plymouth (June, 1978), collected by B. F. Matthews, BM(NH) 1984.9.19.368.

(b) From elsewhere

None.

(ii) NE Atlantic records from the literature

From the gut

None.

Free in body-cavity

Blennius pholis [body-cavity] (Single specimen). Widemouth, Bude, Cornwall, England (Nov.). Matthews (1982*b*: appendix; as *L. furcolabiata*).

Ciliata mustela [body-cavity] Wembury Bay, Plymouth, Devon, England. (Sept., 1932), E. I. Jones (1933: 248; as *Ceratotrema furcolabiata*); (March–Sept.), Matthews (1982*b*: 25; as *L. furcolabiata*).

Encapsulated on viscera

Due to their proximity to the records of *L. furcolabiatum*, the following are treated as questionable records of this species, although some, at least, may be *L. rufoviride*. See also *L. rufoviride* and *Synaptobothrium caudiporum* for further questionable records.

(?) *Blennius pholis* [viscera, liver] Plymouth, Devon, England. Nicoll (1914: 485; as *L. rufoviride*).

(?)—— [peritoneum] Wembury Bay, Plymouth, Devon, England (June–Dec.). Matthews (1982*b*; 24; as 'hemiurid metacercariae').

(?) *Gaidropsarus mediterraneus* [body-cavity] Wembury Bay, Plymouth, Devon, England; Heybrook Bay, Plymouth; Widemouth, Bude, Cornwall, England (May, June). Matthews (1982*b*; appendix; as 'hemiurid metacercariae').

(?) *Gobius paganellus* [peritoneum] Wembury Bay, Plymouth, Devon, England. Matthews (1982*b*: 24; as 'hemiurid metacercariae').

(?) *Labrus bergylta* [liver, intestinal wall] Plymouth, Devon, England. Nicoll (1914: 486; as *L. rufoviride*).

(?) *Symphodus melops* [body-cavity] Wembury Bay, Plymouth, Devon, England (Jul., Nov.). Matthews (1982*b*: appendix; as 'hemiurid metacercariae').

(?) *Taurulus bubalis* [body-cavity] Bovisand, Plymouth, Devon, England; Widemouth, Bude, Cornwall, England. (May–Nov.) Matthews (1982*b*: appendix; as 'hemiurid metacercariae').

ASPECTS OF BIOLOGY. Although previously reported by only two authors and known from only a small number of localities, this parasite may occur in large numbers in these localities. Our studies indicate that its distribution may be limited to the south-west region of the British Isles: most records are from the region of Plymouth, Devon, but it also occurs in Cornwall, the Isles of Scilly, Co. Galway, Eire, possibly Co. Wexford, Eire, and one specimen has been observed in Cardigan Bay, Wales by Dr A. Jones (pers. comm.).

The most frequently found adult form occurs living freely in the body-cavity of the rockling *Ciliata mustela,* although small numbers of worms have been recovered from the stomach of *Conger conger* and on two occasions large numbers were obtained from the stomach of *Anguilla anguilla.* The records indicate that this is essentially a rock-pool species, occurring in the body-cavity of the five-bearded rockling, but capable of survival in the gut of eels. It is acquired by feeding upon small rock-pool fishes, such as blennies, gobies and labrids, which harbour encapsulated, small, immature or often ovigerous forms. Our electrophoretic studies (Gibson *et al.,* 1985) indicate that the larval form is *Cercaria vaullegeardi* Pelseneer *sensu* Matthews (1980, 1981*a,b,* 1982*b*). Matthews' work indicates that the cercaria is released from the mollusc *Gibbula umbilicalis* via a specialized, tubular, anterior region of the daughter-sporocyst which serves to transport it to the exterior through the gill-filaments of this mollusc. Matthews has described in detail the development and emergence of the cercaria and the complex inoculation whereby it penetrates the copepod second intermediate host, in this case *Tigriopsis brevicornis,* which harbours the metacercaria.

It is worth noting that specimens from the body-cavity of *Ciliata mustela* do not normally appear to lay eggs, which remain within the gravid uterus in large numbers. When such specimens are dropped into sea-water a stream of eggs is immediately released (B. F. Matthews, pers. comm.). It would appear, therefore, that transmission occurs when the rockling is eaten by a predator or when it dies and is broken down. These worms can do considerable damage to the liver of the rockling, as they appear to browse freely upon it, often in large numbers. In cases where liver-damage is great, there appears to be some release of eggs, as some have been recovered from bile in the gall-bladder (B. F. Matthews, pers. comm.).

Previous descriptions. E. I. Jones (1933: 248; as *Ceratotrema furcolabiata*).

Description (Figs 14, 15, 16C,D, 17) (a) *Adult form.* Eighteen whole-mounts and nine sets of serial sections from *Ciliata mustela,* four whole-mounts and one set of sections from *Anguilla anguilla,* and one set of serial sections (initially studied as a whole-mount) from *Conger conger* were available for study. Since most aspects of the morphology of this worm are not distinguishable from those of *L. rufoviride,* it will not be described in detail: only the points of difference will be commented upon, although the worm is adequately figured and the dimensions given in Table 10.

Specimens from all three hosts mentioned above are morphologically very similar (Figs 14, 15), all having the characteristic pair of protrusions ('horns') on the pre-oral lobe, although these may not be fully developed in very small, immature forms. It is noticeable, however, that, as with *L. musculus,* the ecsoma tends only to be protruded in forms from the gut (Fig. 14C) (although it may be forced out in squashed preparations: Fig. 14A) and that, as in the case of *L. rufoviride,* specimens from *A. anguilla* tend to be smaller. The most obvious difference between specimens from different hosts is that, as also occurs in *L. musculus,* those forms from the body-cavity tend to have hypertrophied gonads and uterus, resulting in their being broader. One feature, common to worms from all three hosts, is that, compared with *L. rufoviride,* the papillae around the oral sucker are well developed (Fig. 16C,D).

(b) *Encapsulated form* These small worms (Fig. 17) from the viscera of blennies, gobies, etc., are encapsulated by a layer of fibrous tissue of host origin. Within the capsule the worms appear to be active and to feed upon the capsule-wall. In morphology (see Table 10 for dimensions) they are very similar to the smallest specimens recovered from the body-cavity of rockling. Some of the worms are ovigerous and in some cases developing 'horns' can be seen.

Discussion. *Ceratotrema furcolabiata* from the body-cavity of *Ciliata mustela* at Wembury Bay, Plymouth, was described as a new genus and species by E. I. Jones (1933). The genus *Ceratotrema* (erroneously called *Jajonetta* by Jones on p. 252 of his paper) was synonymized with *Lecithochirium* independently by Dawes (1947) and Manter (1947), who retained the species as valid. This synonymity was accepted by Gibson & Bray (1979), although Yamaguti (1971) had accepted *Ceratotrema* as valid and Skrjabin & Guschanskaja (1955*a*) had gone as far as to erect a new tribe for this genus and *Dissosaccus* on the mistaken belief that an ejaculatory (prostatic)

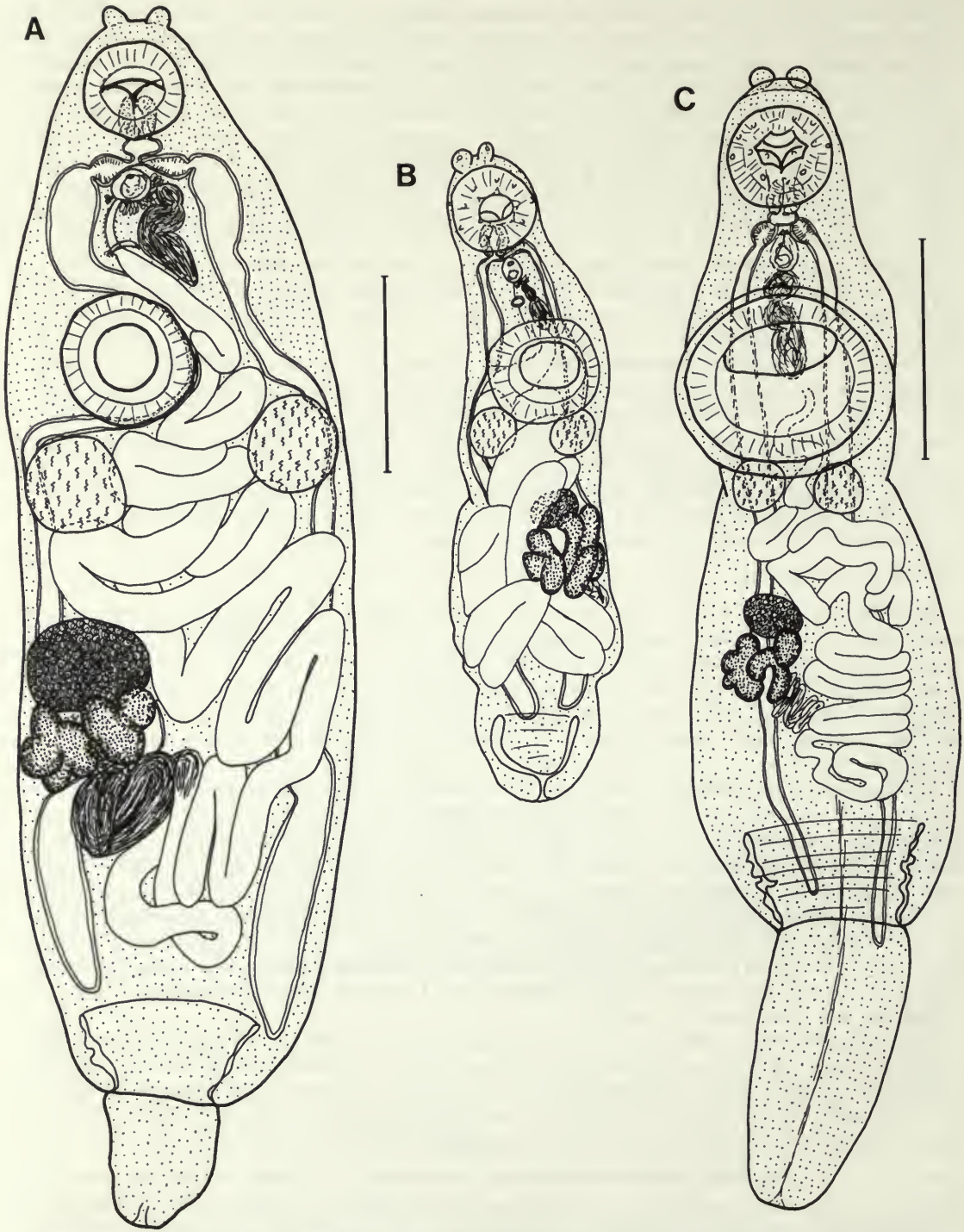
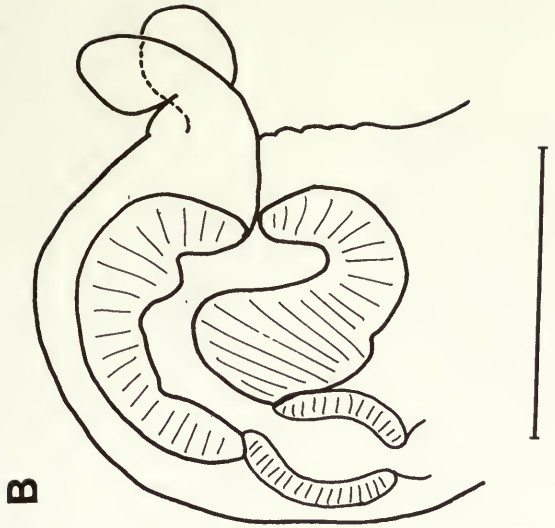


Fig. 14 *Lecithochirium furcolabiatum*. (A) Flattened specimen, ex body-cavity of *Ciliata mustela* (ecsoma forced out); (B) Entire worm, ex body-cavity of *C. mustela*; (C) Entire worm, ex stomach *Anguilla anguilla*, Isles of Scilly. Scale bars: 1 mm.

Fig. 15 *Lecithochirium furcolabiatum*. (A) Sagittal section of forebody, ex *Anguilla anguilla*; (B) Lateral view of anterior extremity, ex *Conger conger*. Scale bars: A 300 μm; B 500 μm.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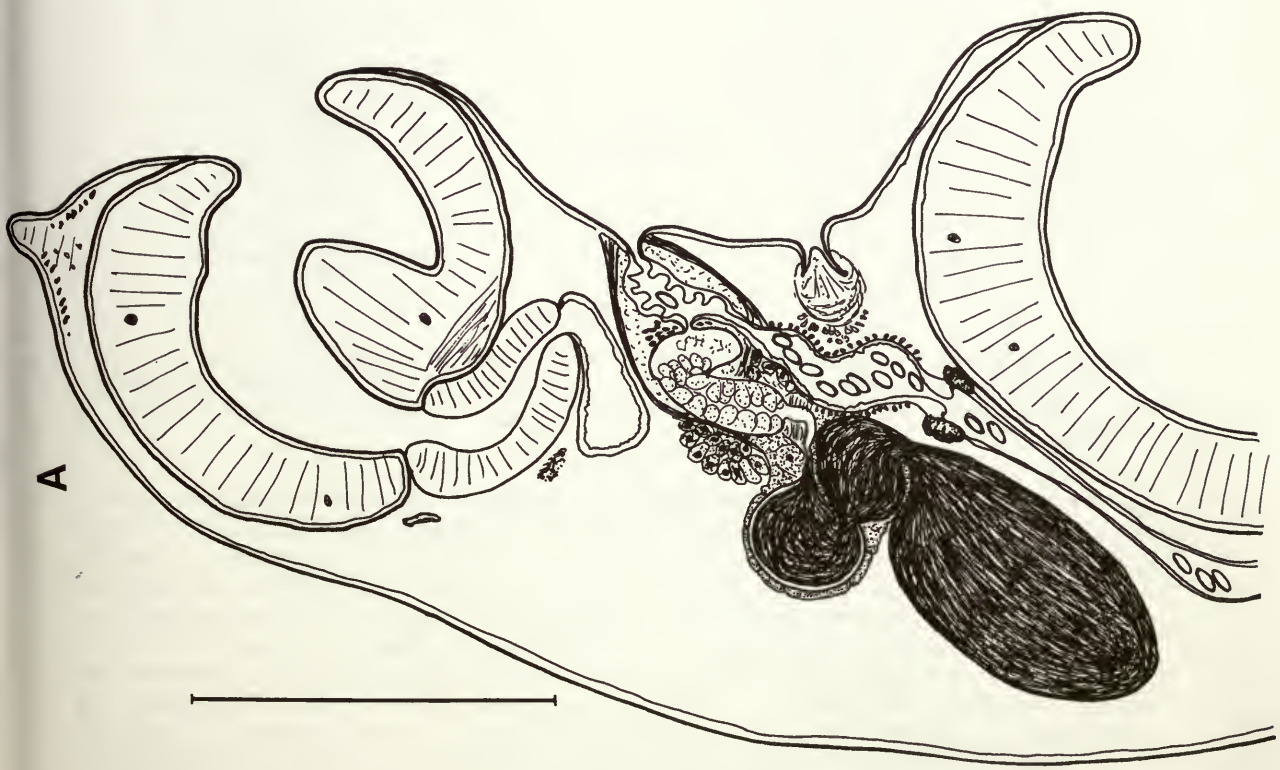
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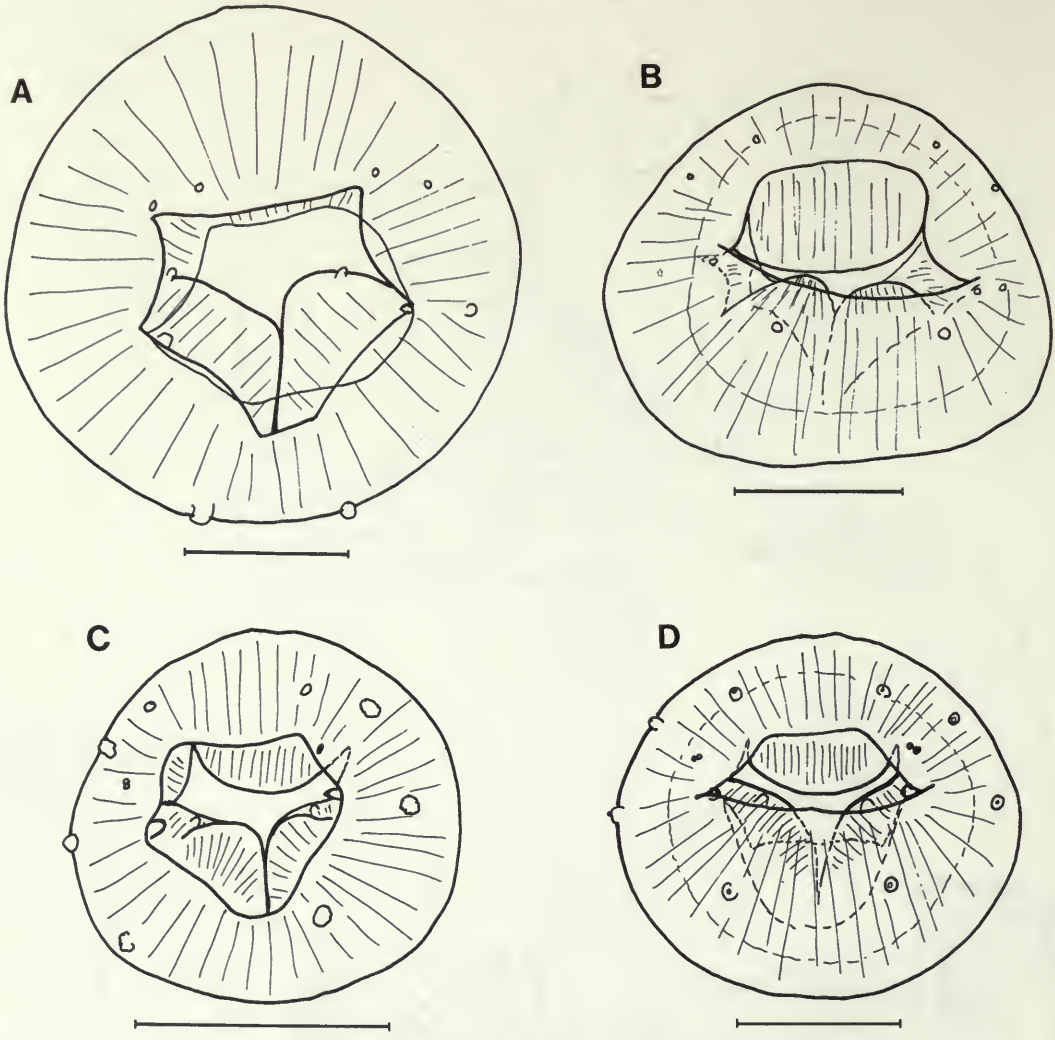

Fig. 16 Oral sucker of two *Lecithochirium* spp. showing arrangement of papillae. (A) *L. rufoviride* ex *Conger conger*, Moray Firth; (B) *L. rufoviride* ex *Anguilla anguilla*, Kristineberg; (C) *L. furcolabiatum* ex *Ciliata mustela*, Wembury Bay; (D) *L. furcolabiatum* ex *A. anguilla*, Isles of Scilly. Scale bars: 200 μm.

vesicle is not present. Of the differences listed by Jones between *Ceratotrema* and *Lecithochirium*, only the bifid nature of the pre-oral lobe seems really worthy of serious consideration. It is worth noting that he makes a special point of the large size of his greatly flattened worms, giving the range as 7·3 to 7·8 mm, and yet the type-specimen in the Collection of the BM(NH) measures only 4·5 mm (Table 10), which compares favourably with our material from the type-host and type-locality. Our observations indicate that, in addition to the shape of the pre-oral lobe, the only significant differences between *L. furcolabiatum* and *L. rufoviride* are better-developed papillae around the oral sucker (Fig. 16) and, only in the case of forms from the body-cavity, the hypertrophy of the gonads and uterus and the permanent withdrawal of the ecsoma. As indicated in the case of *L. musculus* (see below), it seems likely that the hypertrophy of the gonads and uterus is associated with the site of the parasite and the necessity for storage of a large number of eggs (eggs released into the body-cavity would be encapsulated and destroyed) and perhaps the

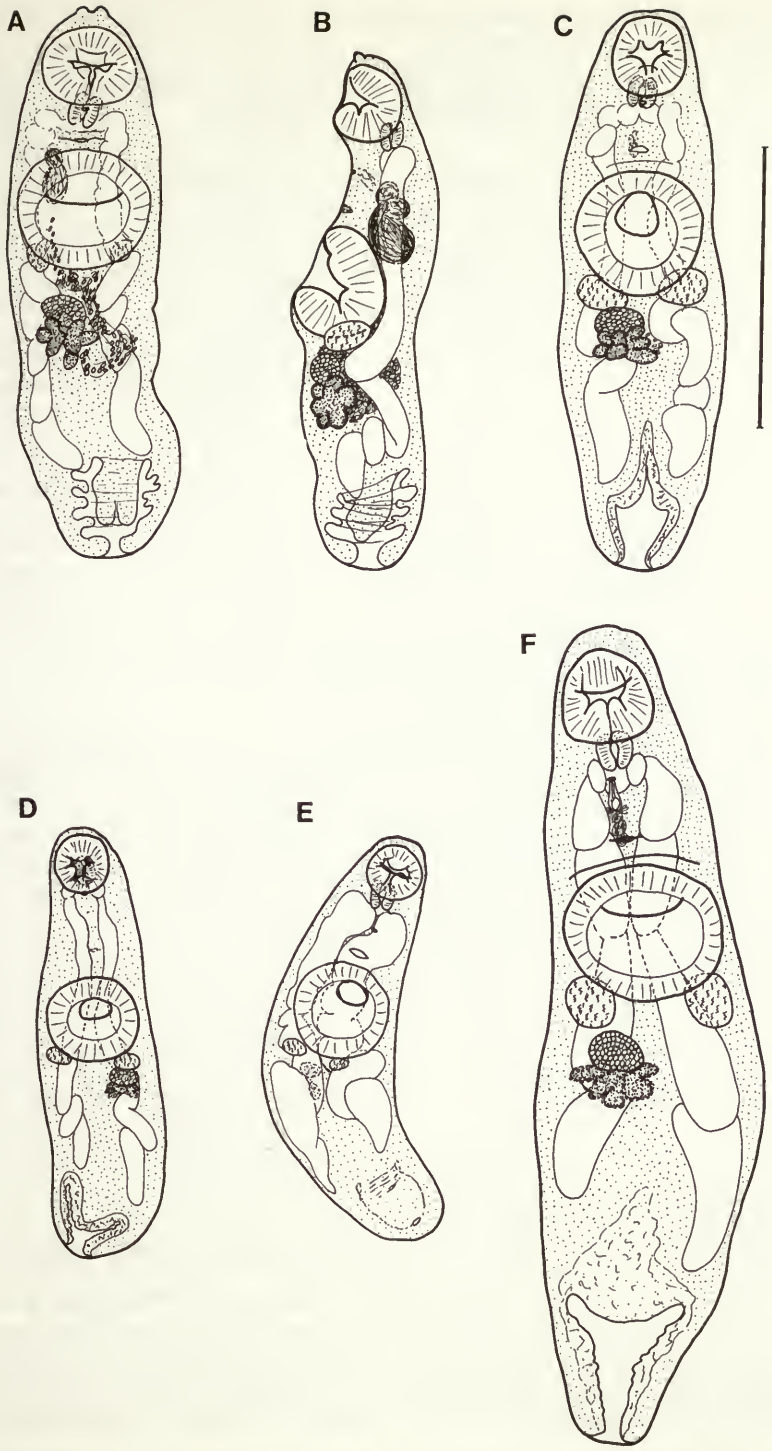

Fig. 17 Young forms of *Lecithochirium*. (A,B,D) *L. furcolabiatum* encysted in *Blennius pholis*, Wembury Bay; (C) *L. furcolabiatum* free in body-cavity of *Ciliata mustela*, Wembury Bay; (E) *L. ? furcolabiatum* encysted in *Coryphoblennius galerita*, Galway; (F) *L. rufoviride* ex stomach of *Conger conger*. Scale bars: 1 mm.

Table 10 Measurements of *Lecithochirium furcolabiatum*

Authority Host Locality	E. I. Jones (1933) *Ciliata mustela* Plymouth	Present material *Ciliata mustela* Devon, Cornwall	Present material *Anguilla anguilla* Isles of Scilly	Present material Encapsulated in *Gobius, Pholis, Taurulus* Plymouth
Length (mm)	7·7(4·5)	1·0–6·25	3·4–5·25	0·7–1·55
Breadth (mm)	1·7(1·45)	0·3–1·9	0·8–1·2	0·21–0·58
Ecsoma (mm)	withdrawn	withdrawn*	0–1·35	withdrawn
Forebody (mm)	–(1·15)	0·28–1·4	0·8–1·0	0·20–0·40
Oral sucker (mm)	0·57 diam. (0·41 × 0·46)	0·14–0·53 × 0·13–0·51	0·34–0·47 × 0·4–0·52	0·11–0·26 × 0·11–0·24
Ventral sucker (mm)	0·77 diam. (0·62 × 0·63)	0·23–0·79 × 0·21–0·8	0·6–0·8 × 0·64–0·86	0·17–0·38 × 0·17–0·36
Sucker-ratio	–(1 : 1·37)	1 : 1·32–1·83	1 : 1·16–1·8	1 : 1·5–1·73
Testes (mm)	0·72 × 0·45 (0·64 × 0·35)	0·06–0·65 × 0·07–0·52	0·16–0·24 × 0·17–0·24	0·04–0·13 × 0·07–0·16
Ovary (mm)	0·51 diam. (0·27 × 0·54)	0·05–0·52 × 0·07–0·62	0·2–0·24 × 0·26–0·33	0·05–0·12 × 0·06–0·14
Eggs (μm)	23 × 11(21 × 12)	21–23 × 12–15	22–25 × 12–15	19–22 × 11–12

The figures in parentheses are measurements of the type-specimen in the BM(NH) Collection.
*The ecsoma is forced out in some flattened preparations.

accelerated production of eggs if the rockling dies or is eaten by an unsuitable host. Similarly, the physico-chemical conditions of the site, as in the case of *L. musculus,* may well be responsible for the non-eversion of the ecsoma. Since hypertrophy of the gonads does not occur in specimens of *L. furcolabiatum* from the gut, and as eversion of the ecsoma does take place in these forms, they cannot be considered as valid criteria. The presence of enlarged papillae around the oral sucker and the presence of 'horns' on the pre-oral lobe seem, on their own, of questionable value, especially as the oral papillae have an identical arrangement to those of *L. rufoviride*. Nevertheless, iso-electric focusing studies (Gibson *et al.*, 1985) indicate that certain enzyme-patterns are not shared by the two forms. We, therefore, consider *L. furcolabiatum* to be a distinct species; but it is clear, from its limited distribution and close morphological and biochemical similarity, that it is a form recently derived from *L. rufoviride* and is primarily a rock-pool form particularly adapted to the body-cavity of rockling, although still capable of surviving in the gut of eels. It seems possible that the body-cavity forms of *L. musculus* are moving in the same direction.

Lecithochirium fusiforme Lühe, 1901

(?) *Distomum rufoviride* Rudolphi of Prenant (1886).
Sterrhurus fusiformis (Lühe) Looss, 1907.
Lecithochirium gravidum Looss of Baylis (1928, 1939), Baylis & Jones (1933) and Bray (1973).

TYPE-HOST AND LOCALITY. *Conger conger,* locality unknown. (The species is based upon specimens removed from three vials of *Lecithochirium rufoviride* in the Berlin Museum, including one vial of unknown origin, one donated by Parona and one donated by Wagener. Presumably Parona's came from the Italian coast, and it is worth noting that he worked in Genoa and published a record of '*Apoblema rufoviride*' from *Conger conger* at Venice in 1902.)

RECORDS

(i) Material studied
(a) From the NE Atlantic
Conger conger [?] Locality unknown. BM(NH) 86.9.20.4–12.

—— [stomach] Irish Sea. BM(NH) 1976.4.9.110–113. Material of Rees & Llewellyn (1941: 391; as *Sterrhurus fusiformis*).
—— [stomach] Plymouth, Devon, England. (May, 1932) BM(NH) 1932.11.29.22–41. Material of Baylis & Jones (1933: 631; as *L. gravidum*); Baylis (1939: 48; as *L. gravidum*); and Bray (1973: 178; as *L. gravidum*). Material collected by M. Rothschild BM(NH) 1932.11.22.57–58. Material collected by J. S. Steward BM(NH) 1938.11.4. 228–240.
—— [stomach] Guernsey, Channel Islands (July) BM(NH) 1924.3.15.53–67. Material of Baylis (1928: 322; as *L. gravidum*) and Bray (1973: 178; as *L. gravidum*).
—— [stomach] Northern Bay of Biscay (47°N, 06°W; depth 330–610 m; Jan., 1971). BM(NH) 1973.5.17.63–65. Material of Bray (1973: 178; as *L. gravidum*).
—— [gut] Lowestoft, Suffolk, England. Collected by J. Mahon. BM(NH) 1980.7.25.30–39.
—— [gut] Locality unknown. Collected by J. Mahon. BM(NH) 1980.7.25.6–27.

Immature (?) accidental infestations

(?) *Lophius piscatorius* [stomach, intestine] Plymouth, Devon, England (May, 1972). BM(NH) 1984.9.26.1.
(?) *Molva molva* [posterior intestine] Plymouth, Devon, England (May, 1972). BM(NH) 1984.9.26.2.

(b) From elsewhere
None.

(ii) NE Atlantic records from the literature
(?) *Conger conger* [stomach] Locality unknown: examined at Nancy, France. Prenant (1886: 218; as *Distomum rufoviride*).
Conger conger [stomach] Plymouth, Devon, England. Baylis & Jones (1933: 631; as *L. gravidum* and *S. fusiformis**); Baylis (1939: 482; as *L. gravidum* and *S. fusiformis**); Bray (1973: 178; as *L. gravidum*); Matthews (1982*b*: appendix).
—— [stomach] Guernsey, Channel Islands. Baylis (1928: 332; as *L. gravidum*); Bray (1973: 178; as *L. gravidum*).
—— [stomach] Roscoff, Finistère, France. Sproston (1939: 15; as *L. gravidum**); [pharynx and intestine] Sproston (1939: 16; as *S. fusiformis*).
—— [stomach] Irish Atlantic Slope (54°N, 12°W; depth 220–275 m; July, 1939). Rees & Llewellyn (1941: 391: as *S. fusiformis*).
—— [stomach] Irish Sea. Rees & Llewellyn (1941: 391; as *S. fusiformis*).
—— [stomach] Millport, Strathclyde, Scotland. D. O. Jones (1943: 52; as *S. fusiformis*).
—— [stomach] Milford Haven, Dyfed, Wales. D. O. Jones (1943: 52; as *S. fusiformis*).
—— [stomach] Albufeira, Algarve Coast, Portugal (July, 1954). Tendeiro & Valdez (1955: 102; as *S. fusiformis*).
—— [stomach] Northern Bay of Biscay (47°N, 06°W; depth 330–610 m; Jan., 1971). Bray (1973: 178; as *L. gravidum*).
Lophius piscatorius [stomach] Plymouth, Devon, England. Baylis & Jones (1933: 631; as *S. fusiformis*); Baylis (1939: 482; as *S. fusiformis*); Dawes (1947: 286; as *S. fusiformis*).
—— [?] NE Atlantic. Gaevskaja (1978*a*: 83). (Possibly not an original record).

Aspects of biology. Chabaud & Campana-Rouget (1959) claimed that the life-history of this parasite involved larval stages in *Gibbula* and copepods, immature adults in the body-cavity of blennies, gobies and labrids and mature adults in the stomach of *Conger conger*. They believed the cercaria to be *C. vaullegeardi* Pelseneer, 1906. As pointed out on p. 64, however, we consider it more likely that they were dealing with larval and immature specimens of *L. rufoviride*. There appears to be no information available which can be definitely attributed to *L. fusiforme*: this is surprising, considering the records of related species from the body-cavity of small, plankton-feeding teleosts. Our observations on the sucker-ratio, sucker-morphology and shape of the vitellarium, etc., of small specimens from *C. conger* suggest that such immature specimens, if they exist in this species, should be readily distinguishable from related species of *Lecithochirium*.

In addition to *C. conger*, this species has been recorded from two other congrids, *Ariosoma balearicum* and *Gnathophis mystax*, in the Adriatic Sea by Sey (1970). As in the case of *L.*

*Although all of the specimens marked *L. gravidum* from *C. conger* which have been examined, i.e. those initially identified by H. A. Baylis, are in fact *L. fusiforme*, it is very possible that some of this material, such as that of Sproston, may have been *L. rufoviride*, which is commonly found cohabiting with *L. fusiforme*.

rufoviride, there are also a small number of records from the stomach of *Lophius piscatorius*; but it is not known whether all of this material was, like ours, immature.

Like *L. rufoviride*, the distribution of this species also appears to coincide with that of its major definitive host, *C. conger*, although the records suggest that it does not extend quite as far north as *L. rufoviride*: we only found the latter species in the Moray Firth, as did J. Thulin (*in litt.*) in *C. conger* off Hirtshalls in the Skagerrak. We note that there is a record of '*Distoma grandiporum* Rud.' from *C. conger* off Öresund, Sweden by Olsson (1876); but his description of the vitellarium suggests that it is more likely to have been *L. rufoviride* than *L. fusiforme*. The southern limit of this species appears to be the Azores, although Fischthal & Thomas (1972*b*) claim to have found it in a muraenid eel off Ghana. As with the case of American records attributed to *L. fusiforme* (as *Sterrhurus fusiformis*), we believe that the latter specimens are not conspecific with the European form (see below).

Previous descriptions. Lühe (1901: 476); Looss (1908: 43; as *Sterrhurus fusiformis*); Mathias (1934: 574; as *S. fusiformis*); D. O. Jones (1943: 52; as *S. fusiformis*); Dawes (1947: 286; as *S. fusiformis*); Janiszewska (1953: 30; as *S. fusiformis*; measurements only); Chabaud & Campana-Rouget (1959: 168; *S. fusiformis*; figure only); Bray (1973: 178; as *L. gravidum*; measurements only).

Description (Figs 18, 19). This description is based upon 16 whole-mounts and two sectioned specimens from *Conger conger*. The body of this large hemiurid is fusiform, the *ecsoma* usually being withdrawn or only partly extruded in fixed specimens (Fig. 18). For measurements see Table 11. The ecsomal pore is ventro-terminal. When the ecsoma is completely withdrawn, it may cease to exist as such and its wall becomes part of the thickened, convoluted lining of the ecsomal cavity. The latter cavity usually extends further anteriorly dorsally than it does ventrally. The body-surface is smooth, like many of the species of this group; but, when the ecsoma is withdrawn, the surface of the ecsomal cavity is covered with minute, claviform protrusions. The *oral sucker* is ventrally subterminal, there being only a small pre-oral lobe which tends to envelop the anterior margin of the sucker ventrally. The oral sucker is much smaller than the globular *ventral sucker* (ratio 1 : 1·7–2·5). (It is worth noting that Bray, 1973, using 30 specimens from two lots of material, found a narrower range of 1 : 1·72–2·38 and his results suggested that there was no allometric growth involved. Although our results from a smaller number of whole-mounted specimens indicate that allometry might occur, the ratios ranging in size from 1 : 1·7–1·8 in specimens of 1–2 mm, 1 : 1·85–2·25 in specimens of 1–4 mm, and 1 : 2·0–2·5 in specimens of more than 4 mm, this observation is questionable as our material is from a wide variety of sources and is in various states of preservation, contraction and compression.) The ventral sucker is situated at about one-quarter of the body-length from the anterior extremity.

There is no prepharynx; but the *pharynx* is quite large in relation to the size of the oral sucker and leads into a transversely oval oesophagus. This, in turn, opens posteriorly through a muscular sphincter into a narrow, transverse commissure which links the two large 'Drüsenmagen' situated postero-laterally to the pharynx. These organs appear to be separated from the remainder of the caeca by sphincters which are surrounded by small gland-cells. The dilate caeca pass back from the 'shoulder-region' dorso-laterally and terminate blindly close to the base of the ecsoma or just inside it when it is everted.

The excretory pore is situated terminally on the ecsoma. It leads into a Y-shaped *excretory vesicle*, the tubular stem of which extends forwards, following a sinuous course dorso-medially to the ovarian complex. In contracted specimens the posterior region of the stem may be very convoluted posterior to the uterine field and ventral to the ecsomal cavity. It divides at about the level of the testes, and the two narrow arms pass dorso-laterally into the forebody. According to Looss (1908), these unite dorsally to the pharynx; but, in our material, we were unable to follow them far into the forebody and unable to recognize a commissure in our sections.

The two symmetrical or slightly oblique, oval *testes* are present laterally or ventro-laterally just posterior to the hind margin of the ventral sucker. They occur deep within the body, i.e. they are less ventrally situated than in the case of *L. rufoviride*, although they may occur quite close to the

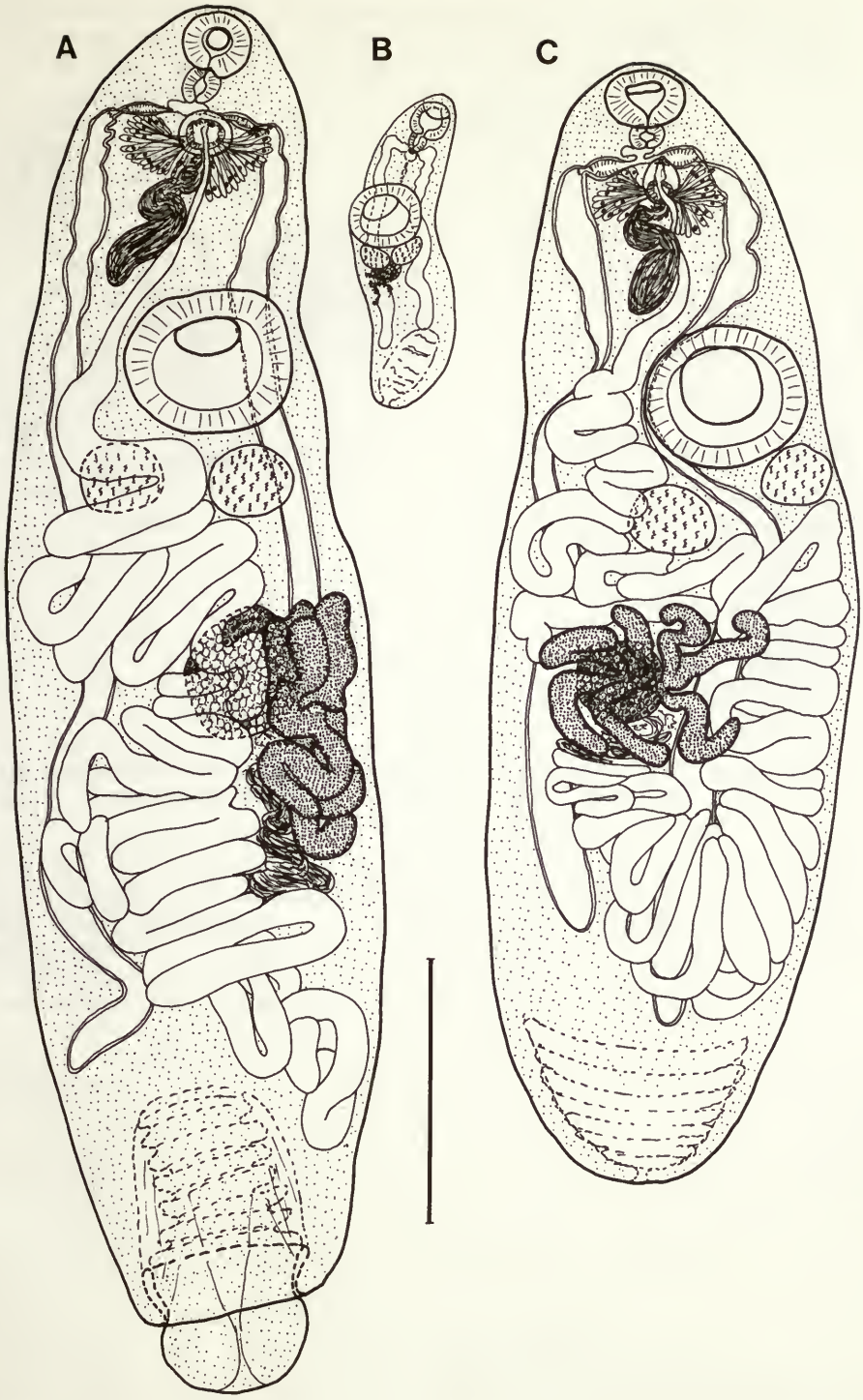

Fig. 18 *Lecithochirium fusiforme*. (A, B, C) Flattened worms, ex *Conger conger* (position of gut, uterus and ventral sucker distorted). Scale bar: 1 mm.

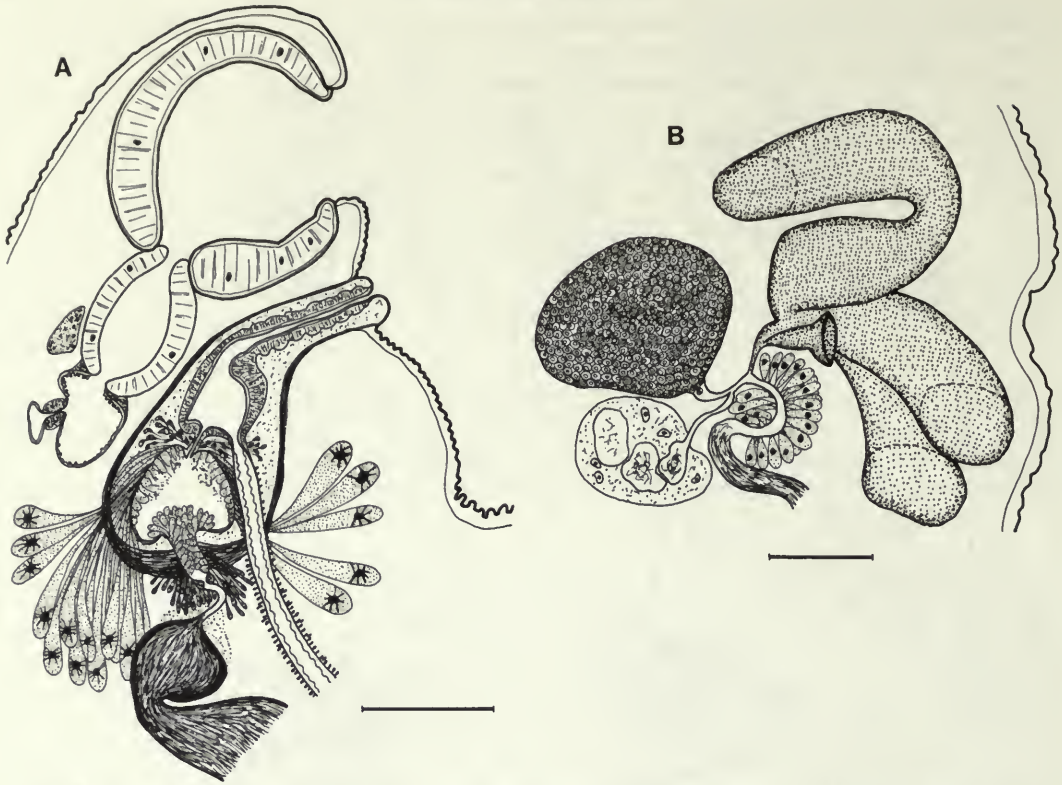

Fig. 19 *Lecithochirium fusiforme* ex *Conger conger* (contracted specimen). (A) Sagittal section of forebody; (B) Lateral view of ovarian complex. Scale bars: 100 μm.

Table 11 Measurements of *Lecithochirium fusiforme* from *Conger conger*

Authority	Looss (1908)	Mathias (1934)	D. O. Jones (1943)	Present material
Name used	*Sterrhurus fusiformis*	*Sterrhurus fusiformis*	*Sterrhurus fusiformis*	*Lecithochirium fusiforme*
Locality	?	Banyuls, South of France	Millport & Milford Haven U.K.	NE Atlantic
Length (mm)	up to 3·65	3·1–6·0	5	1·1–5·5
Breadth (mm)	0·7	1·2–1·85	1·7	0·37–1·9
Ecsoma (mm)*	–	–	0–0·35	–
Forebody (mm)	–	–	–	0·35–1·1
Oral sucker (mm)	0·25–0·3 diam.	0·2–0·3 diam.	0·28 diam.	0·13–0·28 × 0·15–0·35
Ventral sucker (mm)	0·5–0·6 diam.	0·62–0·7 diam.	0·6 diam.	0·27–0·65 × 0·27–0·8
Sucker-ratio	–	–	1 : 2	1 : 1·7–2·5
Testes (mm)	–	0·13–0·21 × 0·17–0·31	0·25 × 0·31	0·1–0·35 × 0·11–0·34
Ovary (mm)	–	0·14–0·24 × 0·36–0·44	0·33 × 0·37	0·08–0·36 × 0·1–0·5
Eggs (μm)	20–23 × 17–19	18–23 × 13–18	24 × 18	23–28 × 15–18

*The ecsoma is normally withdrawn in unflattened, conventionally fixed worms, but may form up to half the length of the worm in live specimens according to Jones (1943).

lateral surface of the body. The vasa efferentia are not visible in our material. The seminal vesicle is variable in shape and size, sometimes being entirely within the forebody and sometimes extending to the level of the middle of the ventral sucker. It is essentially bipartite, although the large, elongate-saccular, proximal part is usually constricted and curved such that its anterior third appears to form a distinct oval unit. The small, distal part of the seminal vesicle is tear-shaped, has a slightly more muscular wall than the proximal part and is connected to the pars prostatica by a short, aglandular duct (Fig. 19A). This duct, which is longer than the pars prostatica, appears to be surrounded by cells similar to those which surround the equivalent region in *L. rufoviride*. (Although these cells are not visible in our formalin-fixed sectioned material, in some of the whole-mounts they appear to be present surrounding this duct and the distal region of the distal portion of the seminal vesicle.) At the junction between the aglandular duct and the pars prostatica there is a muscular sphincter. The pars prostatica is very short and relatively dilate, and most of its length actually occurs within the diffuse muscular wall of the sinus-sac which it penetrates. The small gland-cells which invest the pars prostatica surround the base of the sinus-sac and their ducts pass through the diffuse musculature of this organ (Fig. 19A). A well-developed lining of blebs almost fills the lumen of the pars prostatica. Just within the *sinus-sac*, which is a truncated, claviform structure, the pars prostatica opens into a large ejaculatory vesicle. Some of the blebs lining the pars prostatica extend through the aperture into the ejaculatory vesicle and appear to form a distinct covering to the proximal wall of this vesicle (Fig. 19A). Similar blebs line much of the remainder of the ejaculatory vesicle, although apparently separated from the blebs of prostatic origin by a naked region. These distal blebs, which are anuclear and often appear to rupture and release a secretion into the vesicle, are associated with extremely large gland-cells that extend laterally over a great proportion of the breadth of the forebody at the level of the sinus-sac. These 'ejaculatory gland-cells' are much larger than the 'prostatic gland-cells' and are unusual in that their nuclei appear to be connected to the cell-wall by radial strands (Fig. 19A). The narrow ducts from these elongate, distally-tapering cells pass between the muscles in the proximal part of the wall of the sinus-sac, where these muscles are diffuse, and lead toward the wall of the ejaculatory vesicle (Fig. 19A). It seems very likely that the blebs lining the distal part of the ejaculatory vesicle are merely the distal extremities of these large gland-cells. A similar relationship apparently occurs between the blebs lining the pars prostatica and the prostatic gland-cells. Distally the ejaculatory vesicle opens via a narrow sphincter, surrounded by small gland-cells, into a wide, very muscular hermaphroditic duct which receives the metraterm ventrally. The hermaphroditic duct opens through the genital pore, which is situated mid-ventrally at the level of the pharynx, although the degree of contraction makes its position somewhat variable. Presumably, during copulation a temporary sinus-organ is formed by the eversion of the hermaphroditic duct. There appears to be no genital atrium.

The oval *ovary* is present submedially either sinistrally or dextrally deep within the body and a short distance posterior to one of the testes, although normally separated from this testis by coils of the uterus. The short oviduct leaves the ovary posteriorly and passes postero-ventrally, receiving both the duct from Juel's organ and the common vitelline duct immediately prior to its entry into Mehlis' gland (Fig. 19B). Mehlis' gland and Juel's organ are situated immediately postero-ventral and posterior to the ovary, respectively. Posteriorly to the ovarian complex, the first coils of the *uterus* form a uterine seminal receptacle. In our specimens the uterine coils then pass posteriorly on the same side of the body as the ovarian complex to, or almost to, the level of the base of the withdrawn ecsoma, before crossing to the other side of the body and returning anteriorly. They pass forward ventrally to the caecum and laterally to the ovarian complex, but usually loop back across the body between the ovary and the testis on the ovarian side of the body. The amplitude of the coils then reduce as the uterus passes the level of the testes ventrally and usually on the opposite side of the body to the ovarian complex. At about a level between the middle of the ventral sucker and the middle of the seminal vesicle the uterus narrows to form a metraterm, which passes forward ventrally to the seminal vesicle and enters the base of the sinus-sac immediately ventral to the pars prostatica. It should be emphasized that the course of the uterus and the position of some organs can be drastically altered in flattened or contracted

specimens. The uterus contains numerous small, oval eggs. The *vitellarium* is composed of seven digitiform or claviform lobes which often appear to be arranged radially; but, when examined closely, it can be seen to be composed of two closely associated masses, one of three lobes and the other of four. The length of the lobes is in the region of four to six times their breadth, even in the smallest specimens. The middle of the vitellarium is situated immediately postero-ventrally to the ovary, but the lobes often cover this organ ventrally. Short ducts from the two masses unite medially to form a short, narrow common duct which, in turn, unites with the oviduct.

Discussion. It is very possible that *Lecithochirium grandiporum* (Rudolphi, 1819) is a senior synonym of *L. fusiforme*. We can find no significant morphological difference between the two species; but our material, taken from two specimens of *Muraena helena* from the Adriatic and Mediterranean Sea (off Malta) preserved in the Fish Collection of the BM(NH), is not in good condition, the specimen from Malta having been in the Museum since 1855. It would appear, however, that *L. grandiporum* is smaller and has only been recorded from the muraenid eel *Muraena helena* in the Mediterranean Sea (other records by Molin (1859), Olsson (1868; see p. 63) and Linton (1898, 1901, 1905) appear to have been misdeterminations). In fact, this species has only previously been recorded on three occasions: once by Rudolphi (1819) from Naples; once by Looss (1907, 1908) also from Naples; and once by Sey (1970) in the Adriatic Sea. With the exception of two specimens, all of our material was less than 1 mm in length and contained few or no eggs. These specimens ranged in size from 0·6 to 1·4 mm, while the largest of Looss' material, most of which was also immature, reached only 1·6 to 1·7 mm, and Lühe's (1901) measurements of Rudolphi's type-material was 1·8 mm, although Rudolphi himself gave the size as somewhat over 3 mm ($1\frac{1}{2}$ lines). Sey's material has been lost (O. Sey, pers. comm.) and Rudolphi's type-specimens were destroyed during the Second World War (G. Hartwich, pers. comm.). As Lühe (1901) stated that Rudolphi's material was too discoloured to reveal any of the internal details, Looss' (1907, 1908) description and figures and our own material, two specimens of which were sectioned, is all that we have available for any comparisons. Our specimens agree well with Looss' description, although the eggs are slightly longer at 21–23 × 15–17 μm, as opposed to 20 × 15–17 μm. The eggs are, therefore, close to the range of *L. fusiforme* in our material (23–28 × 15–18 μm) and well within that from the literature (18–24 × 13–19 μm). With regard to sucker-ratios and the arrangement of the internal organs, our material compares favourably with our smallest specimens of *L. fusiforme*, even to the extent of the large gland-cells being present surrounding the base of the sinus-sac, although the condition of our material does not reveal whether they are as widespread as in the latter species. It is possible, therefore, that the specimens known as *L. grandiporum* may be stunted specimens of *L. fusiforme* which have entered the wrong definitive host; but, presumably due to the close affinities between these two fish, have been able to develop to maturity, their small size being the result of adverse environmental conditions. This is another problem, however, that must await experimental evidence before a definite answer can be given. As the acceptance of this synonymy would require the replacement of a widely accepted scientific name, we feel that, until more evidence is available, it would be advisable to retain the two species as being distinct.

Nasir & Diaz (1971) listed *Sterrhurus gymnothoracis* Yamaguti, 1940, as a synonym of *L. fusiforme*; but, after examining Yamaguti's type-material, we conclude that the two species are distinct. Apart from the fact that *S. gymnothoracis* has smaller eggs (18–21 × 12 μm (Yamaguti, 1940, 1951); 16–18 × 9–10 μm (Zhukov, 1977); 18–20 × 10–11 μm (our measurements of Yamaguti's types)), it lacks a glandular lining to the ejaculatory vesicle and the large gland-cells which surround the base of the sinus-sac in *L. fusiforme*, and it possesses more distinct prostatic cells.

The specimens reported as *'Sterrhurus fusiformis'* from the western side of the North Atlantic in the Central American region and from the neighbouring region of the North Pacific are not conspecific with the north-east Atlantic form. They differ in that the eggs are much smaller (*c.* 14–18 × 9–12 μm), that their definitive hosts are mainly muraenid rather than congrid eels and that, while they do possess a glandular lining to the ejaculatory vesicle and the related external gland-cells surrounding the base of the sinus-sac, the latter cells are not nearly as widespread as

they are in north-east Atlantic forms. Records of the 'American' form have been made by Linton (1910), Manter (1940, 1947), Hanson (1950), Vigueras (1958), Siddiqi & Cable (1960), Nahhas & Cable (1964) and Rees (1970). We have examined the material of both Linton and Rees. The first available name for this form would appear to be *L. havanensis* (Vigueras, 1958) n. comb. *Ectenurus rodriguesi* Cristofaro & Guimaraes, 1974, from *Gymnothorax vicinus* off the coast of Brazil is probably a synonym of this species.

Fischthal & Thomas (1972*b*) recorded *'S. fusiformis'* from a muraenid eel from off the coast of Ghana. We have examined this material, but it is in too poor a condition for us to pass any opinion.

Lecithochirium musculus (Looss, 1907) Nasir & Diaz, 1971

(?) *Distomum grandiporum* Rudolph of Molin (1859) in part.
Sterrhurus musculus Looss, 1907.
Brachyphallus musculus (Looss) Skrjabin & Guschanskaja, 1955.
Lecithochirium branchialis Stunkard & Nigrelli of Nikolaeva (1966).
(?) *Lecithochirium proterorhini* Naidenova, 1972.
(?) *Lecithochirium ophiocephalus* Naidenova, 1972.
Lecithochirium floridensis (Manter) of Naidenova (1974).
(?) *Hemiurus communis* Odhner of Balozet & Sicart (1960*a*,*b*).

TYPE-HOST AND LOCALITY. *Anguilla anguilla*, Trieste, Italy.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Gobiusculus flavescens [body-cavity] Co. Galway, Eire. (Aug., Sept., Oct., Dec., 1977). BM(NH) 1984.7.13. 11–15. (Material of Collins, 1981: 70).
Pomatoschistus pictus [body-cavity] Co. Galway, Eire. (July, 1977; Jan., 1978). Collected by S. Collins. BM(NH) 1984.7.13.16–17.
Platichthys flesus [stomach] Plymouth, Devon, England (May, 1972). BM(NH) 1984.7.13.18.
—— [intestine] Newton Abbot, Devon, England (Aug., 1959). Collected by S. Markowski. BM(NH) 1965.5.17.14–15.
Salmo trutta [stomach] Mulroy, Co. Donegal, Eire (Sept., Nov., 1980). Collected by E. Fahy. BM(NH) 1981.2.24.1–4 & 1981.11.23.30–39.

Accidental host

Capella gallinago [intestine] Termoncarragh, The Mullet, Co. Mayo, Eire (Sept., 1969). Collected by R. J. Knowles. BM(NH) 1979.4.17.16.

(b) From elsewhere
None.

(ii) NE Atlantic records from the literature
(?) *Anguilla anguilla* [gut] Off Helgoland, North Sea. Tesch (1973 (1977): 353).
(?) —— [stomach] Catchment area of River Garonne, near Toulouse, France. Balozet & Sicart (1960*a*: 105; 1960*b*: 44; as *Hemiurus communis*; see Dollfus, 1962: 586).
(?) *Conger conger* [pharynx] Roscoff, Finistère, France (June, 1937). Sproston (1939: 16).
Gobiusculus flavescens [on liver] Co. Galway, Eire. Collins (1981: 70).
(?) *Trisopterus luscus* [intestine] Roscoff, Finistère, France (June, 1937). Sproston (1939: 11).

ASPECTS OF BIOLOGY. Little is known about the biology of this species. Yamaguti (1934) claimed to have found immature specimens from the tissues of a partly digested gobiid taken from the stomach of *Conger myriaster* off Japan. Most of our specimens also came from the body-cavity of gobiids, so it would appear that these hosts form an integral part of the life-history. Although the evidence suggests that *Anguilla anguilla* is the major definitive host of this parasite in the Mediterranean and Black Seas, a wide range of fishes, which are presumably predators of gobiids, are claimed to harbour it. All of our specimens from gobiids were unencapsulated, motile and in most cases gravid, thus resembling *L. furcolabiatum*.

Records of *L. musculus* outside the Mediterranean and Black Seas and the north-east Atlantic region (i.e. those from Japan, Ghana and the Gulf of Mexico) require confirmation, as there are several nominal species which are morphologically similar to *L. musculus*. In the north-east Atlantic this species has been recorded as far north as the British Isles and, although its southern limit is not known, it would appear to have a Lusitanean distribution.

One interesting feature worthy of comment, in the material which we have studied from the body-cavity of gobiids, is the hypertrophy of the gonads and uterus compared with the same species from the stomach of teleosts (cf. Dollfus, 1962). This same phenomenon is also visible in *L. furcolabiatum,* although not nearly to the same extent. We presume that the distention of the uterus is associated with the release of a large store of eggs when the gobiid host dies or is eaten by an unsuitable definitive host. The eggs are retained in the uterus, as it is likely that any eggs released into the body-cavity would be encapsulated and destroyed. The large size of the gonads, however, is more difficult to explain, unless either they are capable of producing vast numbers of eggs very quickly during the period of survival after the death of the gobiid or in the gut of an unsuitable definitive host. Perhaps it is more likely that the mechanism which causes the hypertrophy of the uterus, permitting the retention of large numbers of eggs, also causes unnecessary hypertrophy of the gonads.

Previous descriptions. Due to the confused situation regarding this and related species, readers are advised to use the descriptions of Looss (1908: 141; as *Sterrhurus musculus*) and Dollfus (1962: 579; as *S. musculus*). Other, more questionable, descriptions which may be consulted include: Vlasenko (1931: 117; as *S. musculus*); Yamaguti (1934: 444; as *S. musculus*); Nikolaeva (1966: 57; as *Brachyphallus musculus*); Nikolaeva & Solonchenko (1970: 141; as *B. musculus*); and Naidenova (1974: 51; as *L. floridensis*): see also Naidenova (1972: 143; as *L. proterorhini*) and Naidenova (1972: 145; as *L. ophiocephalus*).

Description (Figs 20–22). This description is based upon 17 whole-mounted and two serially sectioned specimens from the body-cavities of Irish gobies (see Table 12). These stout, spindle-shaped to almost oval worms have a maximum breadth in about the middle of the body and their posterior extremity is much more blunt than the anterior (Figs 20A, 21). The small *ecsoma* is normally withdrawn in specimens from the body-cavity (we have specimens from the stomach of sea-trout with it extruded: Fig. 21C). Although the body-shape of the majority of specimens is as described above, the smallest specimens, containing few eggs, are similar in shape and internal morphology to the young specimens obtained from the gut of flounders (Fig. 22B). The body-surface is smooth, there being no *plications*. There is no presomatic pit; but the ventral surface of the forebody is concave and in association with this concavity, just anterior to the ventral sucker, there is often a distinct, transverse ventro-cervical groove (Fig. 20B).

The small *oral sucker* is ventrally subterminal and surmounted by a small pre-oral lobe. The globular *ventral sucker* is situated at about one-third of the body-length from the anterior end, and, although about twice the diameter of the oral sucker, in the gravid specimens from the body-cavity of gobies, it is relatively small in comparison with the width of the body. There is no prepharynx; but the muscular *pharynx*, which is quite large in relation to the size of the oral sucker, leads into a small, but distinct, oesophagus. The latter organ, which may be very wide to slightly elongate, leads posteriorly to dorsally, and gives rise terminally to two short, lateral ducts. These, in turn, open into indistinct 'Drüsenmagen', from which the often wide caeca pass back sinuously into the hindbody in the dorso-lateral fields and end blindly close to the base of the withdrawn ecsoma.

The excretory pore is present terminally on the ecsoma. This opens into a tubular, Y-shaped *excretory vesicle* with a relatively wide stem which extends forward medially to about the level of the testes. Here it divides to form two narrow arms that pass into the forebody in the dorso-lateral field. They appear to unite dorsally to the pharynx.

The two large, subglobular to almost rectangular, triangular or cardioid *testes* are positioned symmetrically to obliquely just posterior to the ventral sucker in the ventro-lateral fields. Their large size in highly gravid worms from the body-cavity of gobies results in them being juxtaposed and almost filling the entire width of the body. The vasa efferentia were not visible in our sections.

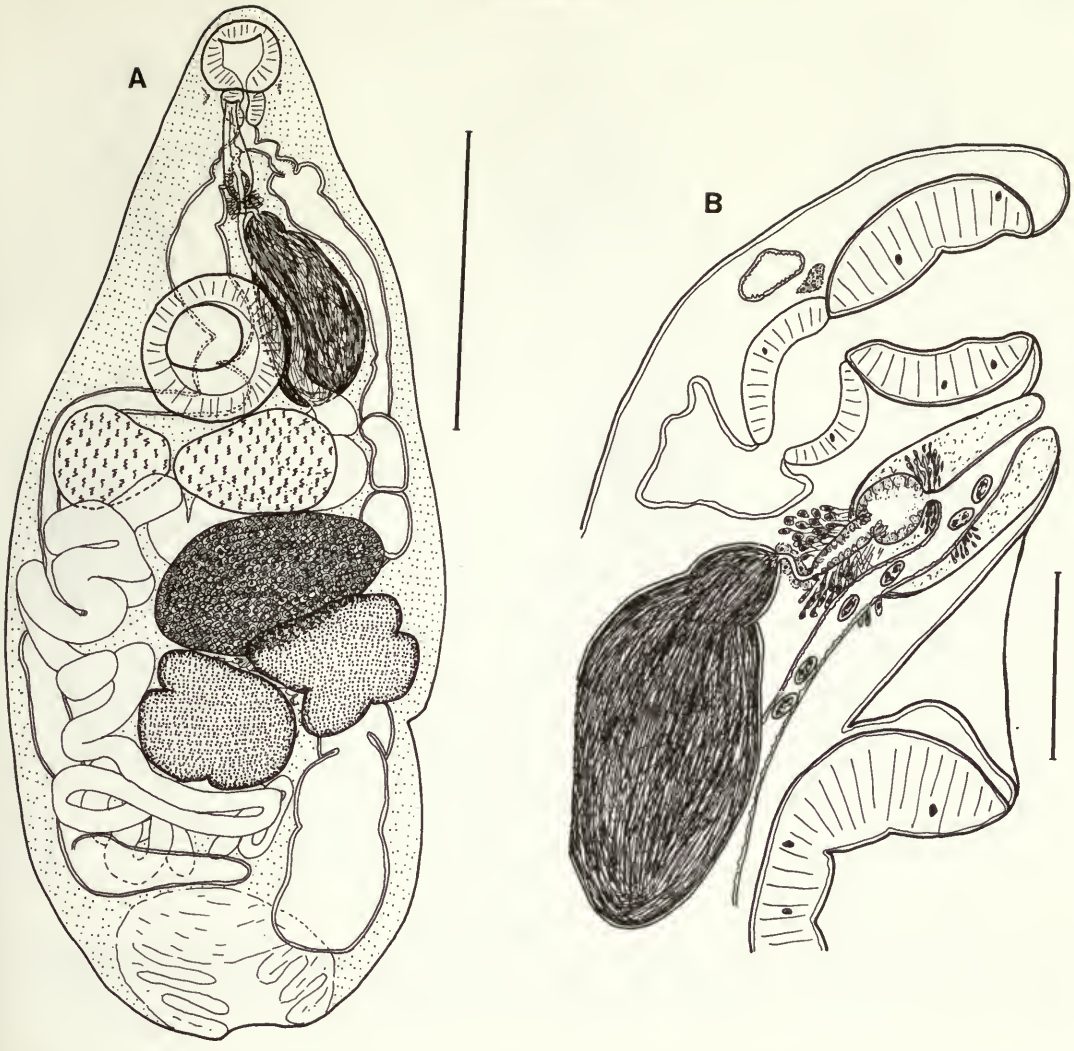

Fig. 20 *Lecithochirium musculus*. (A) Entire worm, ex body-cavity of *Gobiusculus flavescens*, Galway; (B) Composite drawing of sagittal section of forebody: details of terminal genitalia from specimen ex body-cavity of *Pomatoschistus pictus:* outline of specimen ex gut of *Platichthys flesus*, Devon. Scale bars: A 500 μm; B 100 μm.

The seminal vesicle is variable in size and shape, depending upon its contents. It is, however, usually very large, extending back to the posterior margin of the ventral sucker or, occasionally, beyond it. Sometimes, when almost empty, it may be entirely within the forebody. When full of spermatozoa, it may be elongate-oval and undifferentiated into regions, except that it narrows distally to form a short duct which links it with the pars prostatica. The seminal vesicle is in reality, however, bipartite, as the proximal portion is usually distinguishable as a slightly narrower region (Fig. 20B) and may even be constricted off. When not replete with spermatozoa the seminal vesicle is usually wide proximally, but the distal part may be narrow, almost tubular and occasionally convoluted. The duct linking the seminal vesicle with the pars prostatica is surrounded by the same type of non-staining cells as occur in related species. The pars prostatica is short and tubular, but relatively wide. It is surrounded by gland-cells and lined by typical blebs.

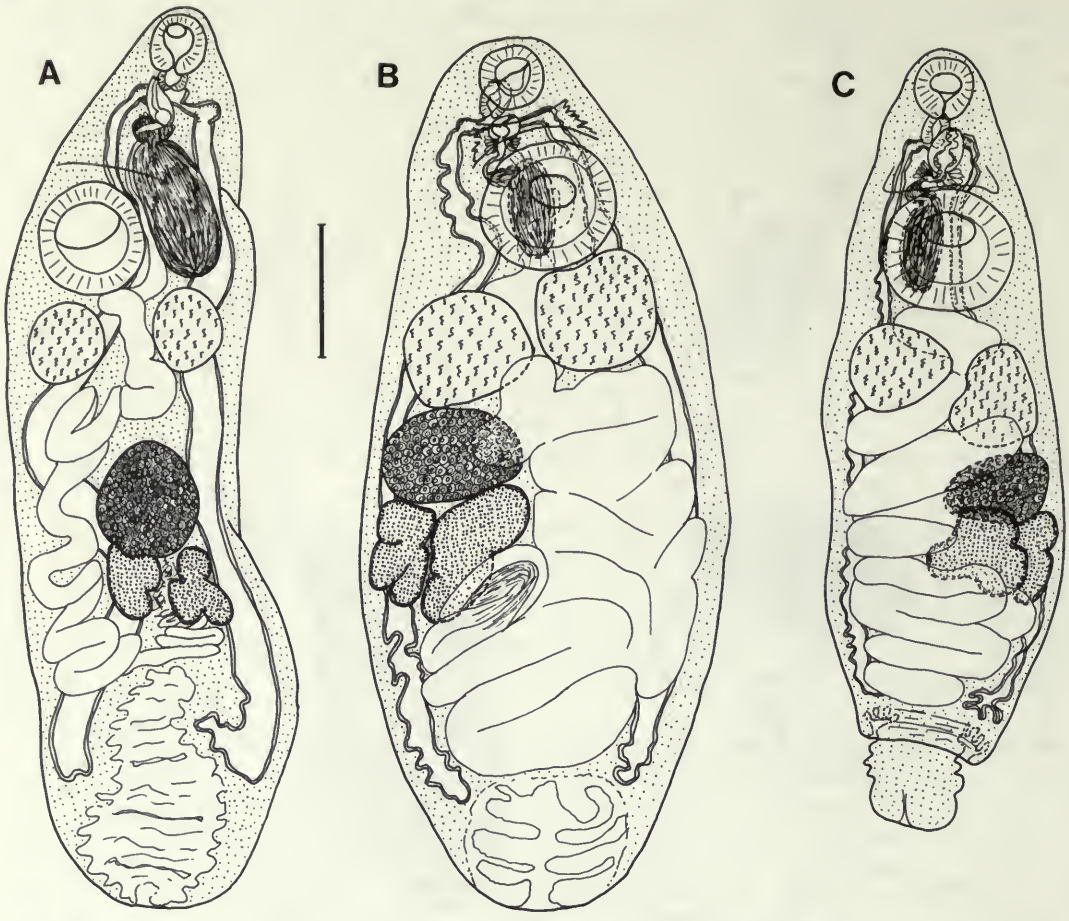

Fig. 21 *Lecithochirium musculus* ex stomach of *Salmo trutta,* Donegal. (A,B,C) Variations in morphology. Scale bar: 300 μm.

It enters the base of the relatively large, although weakly developed, claviform *sinus-sac,* whereupon it opens into a distinct, glandular ejaculatory vesicle, i.e. it possesses a blistered lining proximally and laterally: these blisters appear to be indistinguishable from and a continuation of the blebs lining the pars prostatica (Fig. 20B). Although not clear in our sections, it seems likely that there is some association between the cells surrounding the pars prostatica and the blebs lining the ejaculatory vesicle, as some ducts appear to pass into the base of the sinus-sac. It is also possible, however, that there is some movement of the lining from the pars prostatica into the ejaculatory vesicle. Distally the ejaculatory vesicle unites with the metraterm to form an hermaphroditic duct, which may be straight or sinuous and opens directly through the genital pore. The sphincter uniting the ejaculatory vesicle with the hermaphroditic duct is surrounded by small gland-cells. Occasionally in fixed specimens the hermaphroditic duct is partly everted to form a small temporary sinus-organ. There is no genital atrium. The genital pore is situated mid-ventrally at the level of the pharynx.

The large, oval *ovary* is situated in the ventro-lateral field on either side of the body immediately or a short distance posterior to one of the testes (the ovary is not always as large as that in Fig. 20A, especially in non-gobiid hosts). The short oviduct leaves the ovary posteriorly and receives the duct from Juel's organ and the common vitelline duct prior to entering Mehlis' gland, which is situated immediately posterior to the ovary and dorsal to the vitellarium. The

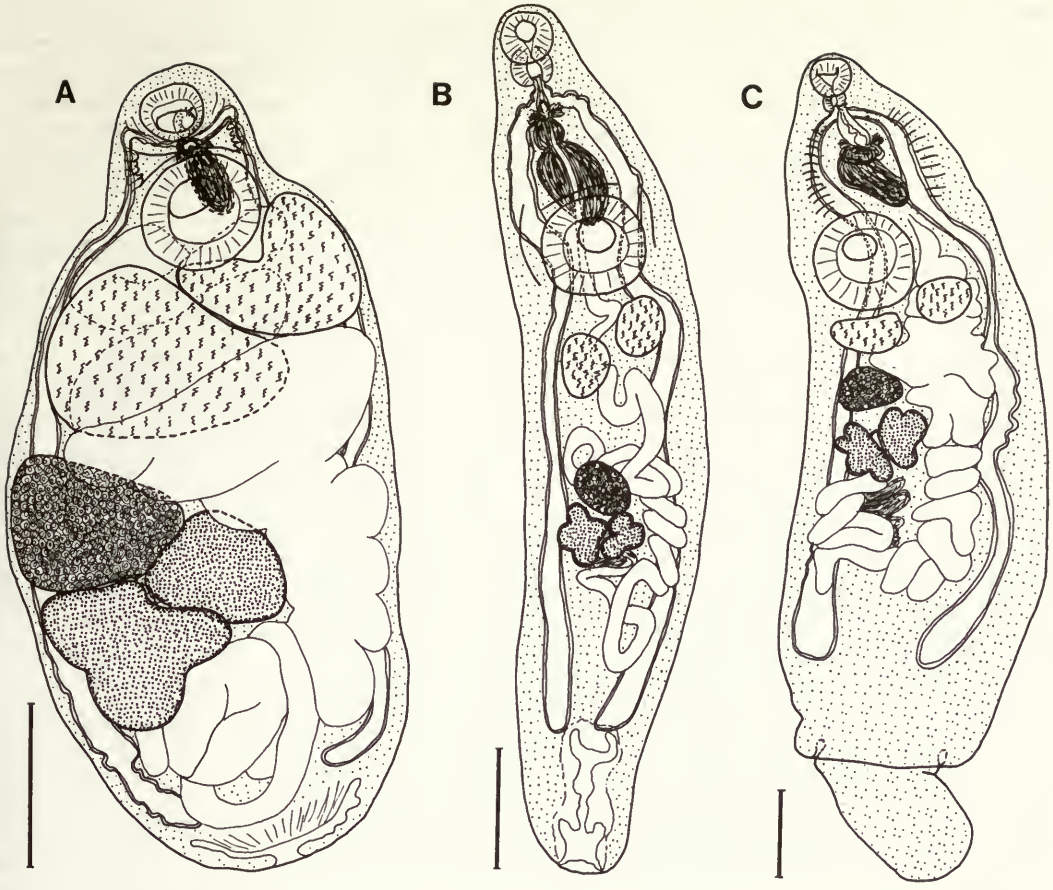

Fig. 22 *Lecithochirium* spp. (A) *L. musculus* with extremely hypertrophied gonads and uterus, ex body-cavity of *Gobiusculus flavescens,* Galway; (B) *L. musculus* with normal gonads and uterus, ex stomach of *Platichthys flesus,* Plymouth; (C) *L. ? floridensis,* ex *Saurida undosquamis,* Egypt. Scale bars: 300 μm.

outer membrane of Juel's organ is very indistinct in our sections, but this organ occurs laterally to Mehlis' gland. Spermatozoa are present in the proximal region of the *uterus* in a small number of specimens; but, although we assume that it occurs, there appears to be no sign of a uterine seminal receptacle in the majority of our worms. The uterine coils pass back laterally from the ovarian complex on the ovarian side of the body to about the level of the withdrawn ecsoma, before returning anteriorly mainly in the dorso-lateral field on the opposite side of the body. At the level of the ovary, the coils, which may be very wide, extend into the ventral field and usually cross the body antero-dorsally to the ovary, passing forward dorsally to the testis on the ovarian side of the body. The uterus then passes more directly forward dorsally or dorso-laterally to the ventral sucker, in the middle of which it narrows to form a muscular metraterm. This duct passes forward ventrally or ventro-laterally to the seminal vesicle and enters the base of the sinus-sac postero-ventrally. The uterus is filled with an enormous number of small, oval eggs. The large *vitellarium* is composed of two symmetrical masses which are situated ventrally on one side of the body immediately posterior to the ovary. The two masses are distinctly or indistinctly lobed, normally with three lobes on one mass and four on the other. The length of the lobes is normally less than their width. Short, medial vitelline ducts unite to form a narrow common duct, which, in turn, unites with the oviduct.

Table 12 Measurements of *Lecithochirium musculus*

Authority	Looss (1908)	Dollfus (1962)	Present material	Present material
Name used	*Sterrhurus musculus*	*Sterrhurus musculus*	*Lecithochirium musculus*	*Lecithochirium musculus*
Host	*Anguilla anguilla, Dentex dentex*	*Anguilla anguilla*	*Gobiusculus flavescens, Pomatoschistus pictus*	*Salmo trutta*
Locality	Adriatic Sea	Etang de Thau, South of France	Co. Galway, Eire	North coast of Eire
Length (mm)	1–1·5	*c.* 1·5	1·1–2·2	0·9–2·1
Breadth (mm)	0·4	*c.* 0·6	0·28–0·75	0·42–0·8
Ecsoma (mm)	–	–	withdrawn	0–0·15
Forebody (mm)	–	–	0·16–0·63	0·2–0·4
Oral sucker (mm)	0·1 diam.	0·12 diam.	0·09–0·13 × 0·09–0·15	0·11–0·14 × 0·11–0·15
Ventral sucker (mm)	0·2 diam.	0·24 diam.	0·2–0·28 × 0·2–0·29	0·2–0·3 × 0·2–0·3
Sucker-ratio	1 : 2	–	1 : 1·85–2·2	1 : 1·77–2
Testes (mm)	–	–	0·08–0·3 × 0·08–0·4	0·06–0·3 × 0·11–0·3
Ovary (mm)	–	–	0·08–0·3 × 0·11–0·42	0·12–0·27 × 0·15–0·32
Vitelline masses (mm)	–	–	up to 0·3 × 0·35	0·1–0·3 × 0·12–0·2
Eggs (μm)	19–21 × 11–13	19–20 × 9–10*	21–26 × 12–14 (usually 23 × 13)	22–24 × 12–15

*23 × 14 μm according to Balozet & Sicart (1960*a*,*b*).

Specimens from the gut of flounders. Four small, ovigerous specimens obtained from the stomach of flounders had a more conventional shape and internal morphology (Fig. 22B). In these specimens the gonads were smaller, the seminal vesicle was distinctly bipartite and the ovary and testes were well separated. The smallest specimens from gobies were similar.

Specimens from the gut of sea-trout. The ten ovigerous specimens studied varied in morphology between forms similar to those from flounders (Fig. 21A) and forms similar to those from gobies (Fig. 21B), although none exhibited the level of gonadal hypertrophy which occurred in some specimens from gobies (Fig. 22A). The ecsoma is protruded in one specimen (Fig. 21C).

Discussion. This species was first described as *Sterrhurus musculus*, the type-species of this genus, by Looss (1907, 1908). He distinguished it from the species of *Lecithochirium* by the absence of a presomatic pit. It was later transferred to the genus *Brachyphallus* Odhner, 1905, by Skrjabin & Guschanskaja (1955*a*), who did not, therefore, recognize *Sterrhurus*, the other species of which they transferred to *Lecithochirium*. Their reason for this action was that they erroneously believed that both *Sterrhurus musculus* and *Brachyphallus crenatus* (Rudolphi, 1802) lacked a sinus-sac (see Figs 20B, 24A). The present species can in fact easily be distinguished from *Brachyphallus* at the generic level by the absence of a plicated tegument. The problem of the validity of *Sterrhurus* was discussed by Gibson & Bray (1979); but Manter & Pritchard (1960*a*), after a review of the problem, concluded that Looss' original distinguishing feature (i.e. the presomatic pit) was the only valid one. Even so, they stated, some of the species 'are still difficult to delineate'. More recently, Nasir & Diaz (1971) argued that the generic value of this criterion was worthless, and, in their revision of *Lecithochirium*, they synonymized the two genera and

made the combination *L. musculus*, although, surprisingly, they considered this species to be a synonym of *L. grandiporum*. In our opinion also, the presomatic pit is not a practical distinguishing feature, as a complete range of intermediate types may be found. Even in the type-species of *Lecithochirium*, the presomatic pit is small and often very difficult to distinguish. We have, therefore, retained *Sterrhurus* as a synonym of *Lecithochirium*.

L. musculus was first described by Looss (1907, 1908) from *Anguilla anguilla* and *Dentex dentex* at Trieste; but he noted that it also occurred in small numbers in *Acipenser sturio, Lichia amia, Psetta maxima, Lophius piscatorius, Gobius niger* and *Ophiodon barbatum*, and that individual specimens had been found in *Trachinus draco, Pagellus erythrinus, Merlangius merlangus, Dicentrarchus labrax* and *Serranus cabrilla*. Since that time it has been recorded on several occasions in the Mediterranean and Adriatic Seas by workers such as Mola (1928), Dollfus (1962), Brinkmann (1966), Nikolaeva (1966), Nikolaeva & Kovaleva (1966), Sey (1970) and Papoutsoglou (1976). It has also been recorded on numerous occasions in the Black Sea by workers such as Vlasenko (1931), Chulkova (1939), Osmanov (1940), Pogorel'tseva (1952), Shulman (1954), Kurashvili (1960), Dolgikh & Naidenova (1968), Kovaleva (1968*a*, 1969, 1970*a,b*) and Nikolaeva & Solonchenko (1970). Outside the Mediterranean region, Black Sea and north-east Atlantic, it is claimed to occur off Japan (Yamaguti, 1934; Ichihara, 1974), in the Gulf of Mexico (Nahhas & Cable, 1964; Nahhas & Short, 1965; Overstreet, 1968, 1969; Nahhas & Powell, 1971), and off the coast of Ghana (Fischthal & Thomas, 1972*b*). With regard to these records, the Japanese specimens have not been fully described, although the few existing measurements fit well. It is difficult, however, to rationalize such a disjunctive distribution, especially when we note that the Japanese form survives in a species of *Conger*, a genus of host from which it has not been recorded for certain in European waters. The records from the Gulf of Mexico result from the synonymy by Manter & Pritchard (1960*a*) of *Sterrhurus floridensis* Manter, 1934 (*sensu stricto*) with *L. musculus*. Manter & Pritchard were of the opinion that the only difference between these species was egg-size, *S. floridensis* reaching a maximum of 17 μm in length and *L. musculus* being 19–21 μm. Since Manter & Pritchard's work more measurements of *L. musculus* are available and these confirm the significantly larger eggs of this species (see Table 12). The confusion mentioned by Manter & Pritchard between species with small or indistinctly lobed vitelline masses is illustrated by the work of Naidenova (1974), who has described a specimen under the name *L. floridensis* (Manter, 1934) from gobies in the Black Sea with an egg-size indistinguishable from *L. musculus*. This confusion would appear to be, at least in part, caused by the uncertain position of *L. musculus* in the Soviet literature. In addition, Nikolaeva (1966) has figured similar material from the Mediterranean Sea under the name *L. branchialis* Stunkard & Nigrelli, 1934, another form from American waters. Naidenova has also described (1972) two new species from gobies in the Black Sea, *L. ophiocephalus* and *L. proterorhini*. These forms also have small lobes on the vitelline masses and an egg-size identical to *L. musculus*. It seems likely that most of these Mediterranean and Black Sea forms are synonyms of *L. musculus*, especially *L. proterorhini* which was recorded from the liver. Nevertheless, to add to the confusion, we have specimens, referred to as *L. floridensis* by Khalil (1981), from *Synodus saurus* and *Saurida undosquamis* from off Alexandria, Egypt (see Fig. 22C), which conform to the morphology of *L. musculus* and yet have eggs of only 15–17 μm in length, i.e. similar to those of *L. floridensis*, to which we provisionally attribute it. *L. floridensis* has been recorded from a species of *Synodus* in the Gulf of Mexico (Manter, 1934, 1947; Sparks, 1957; Corkum, 1959); but there is even confusion with regard to this species, since Corkum (1959) indicated that a presomatic pit is present, and that would put it closer to forms such as *L. synodi* Manter, 1931*. It is clear, therefore, that we cannot for certain relate the European fauna to the American fauna until the situation of the species on that side of the Atlantic has been clarified.

We have examined one young specimen of the material obtained by Fischthal & Thomas (1972*b*) from *Cephalocanthus volitans* off Ghana, but the eggs of this specimen appear to be far too small for it to be *L. musculus*.

*Our specimens from Egyptian Mediterranean waters had no presomatic pit, although the ventral surface of the forebody is deeply concave.

Genus *BRACHYPHALLUS* Odhner, 1905

DIAGNOSTIC FEATURES. Body-surface plicated; plications may be crenulate. Presomatic pit present; circular or oval; deep; glandular. Seminal vesicle bipartite; thin-walled; anterior part small, posterior part large; occurring mostly in forebody. Pars prostatica tubular. Temporary sinus-organ may be seen. Vitellarium two lateral masses; entire, irregularly lobed or indistinctly three- and four-lobed. Parasitic in gut (stomach) of marine and migratory teleosts.

TYPE-SPECIES. *Brachyphallus crenatus* (Rudolphi, 1802) [by original designation].

Brachyphallus crenatus (Rudolphi, 1802) Odhner, 1905

*Fasciola crenata** Rudolphi, 1802.
Distoma crenatum (Rudolphi) Rudolphi, 1809.
Hemiurus crenatus (Rudolphi) Lühe, 1901.
Distoma ocreatum Molin of Olsson (1868) in part, (?) van Beneden (1871) and Linton (1898; 1900, in part; (?) 1901, in part).
Distoma appendiculatum (Rudolphi) of Rudolphi (1819) in part.
(?) *Apoblema appendiculatum* (Rudolphi) of Monticelli (1891) in part.
Hemiurus appendiculatus (Rudolphi) of Stafford (1904) in part (see Miller, 1941) and Willemse (1968) in part.
Distoma ventricosum Rudolphi of Wagener (1860) in part.
Distomum tectum von Linstow, 1873.
Brachyphallus affinis Looss, 1908.
Brachyphallus amuriensis Babaskin, 1928.

TYPE-HOST AND LOCALITY. *Gasterosteus aculeatus,* locality unknown.

RECORDS

(i) Material studied
(a) From the NE Atlantic region
Gasterosteus aculeatus [?] Den Helder, Holland. Zoological Museum, Amsterdam V. Pl. 393.2. Material of Willemse (1968: 85; as *Hemiurus appendiculatus*).
Osmerus eperlanus [?] Wierbalg, Holland. Zoological Museum, Amsterdam V. Pl. 519. Material of Willemse (1968: 85; as *H. appendiculatus*).
—— [stomach] Crouch estuary, Essex, England (Nov., 1979). BM(NH) 1984.1.12.1–2.
—— [stomach] River Ouse at King's Lynn, Norfolk, England (April, 1981). BM(NH) 1983.4.27.30–39.
Platichthys flesus [stomach] Off Aberdeen, Scotland. BM(NH) 1972.3.27.12.
—— [intestine] Morecambe Bay, Lancashire, England. BM(NH) 1962.8.27.71–75. Material of Markowski (1966: 192; as *Hemiurus communis*).
Pleuronectes platessa [?] Firemore, Lock Ewe, Scotland (April, 1967). Collected by K. MacKenzie. BM(NH) 1984.1.12.3.
Reinhardtius hippoglossoides [stomach] Anton Dohrn Bank, Denmark Strait (65°N, 30°W; depth 330–440 m; May, 1974). BM(NH) 1984.1.12.4.
Salmo trutta [?] t'Horntje, Texel, Holland (April, 1961). Zoological Museum, Amsterdam V. Pl. 406.2. Material of Willemse (1968: 84; as *H. appendiculatus*).

(b) From elsewhere
Alosa pseudoharengus [stomach] Passamaquoddy Bay, N.B., Canada (Aug., 1982). BM(NH) 1982.9.28.72.
Clupea harengus [stomach] Passamaquoddy Bay, N.B., Canada (Aug., 1982). BM(NH) 1982.9.28.73–74.
Hippoglossoides platessoides [stomach] Banquereau, off Nova Scotia, Canada (45°N, 57°W; depth 180 m; July, 1976). BM(NH) 1977.2.17.28. Material of Bray (1979: 422).
Reinhardtius hippoglossoides [stomach] Grand Banks, off Newfoundland, Canada (48°N, 50°W; depth 168 m; July, 1976). BM(NH) 1977.2.17.29. Material of Bray (1979: 422).
Salmo salar [stomach] Kaliningrad (Königsberg), U.S.S.R. Material of A. Looss. BM(NH) 1931.10.7.33–34.

*Although *Fasciola salmonis*, which Müller (1780) figured from the intestine of *Salmo* in Denmark, has been mentioned as a synonym of this species, Müller's figures are, in our opinion, unrecognizable.

(ii) NE Atlantic records from the literature

(?) *Ammodytes tobianus* [gills, stomach, intestine] Belgian coast (Aug.). van Beneden (1871: 64; as *Distoma ocreatum*).

(?) —— [?] Scandinavia. Odhner (1905: 355).

—— [stomach, intestine] St. Andrews, Fife, Scotland. Nicoll (1907: 88).

—— [intestine] St. Bride's Haven, Dyfed, Wales (Sept., 1960). Crothers (1966: 24).

Clupea harengus [?] Northern North Sea. Reimer & Jessen (1972: 65).

Conger conger [intestine] Roscoff, Finistère, France (June, 1937). Sproston (1939: 46).

Gadus morhua [?] Western Kattegat to Bornholm in the Baltic Sea. Køie (1981: 61).

Gasterosteus aculeatus [?] West coast of Sweden. Odhner (1905: 354).

(?) —— [?] Greenland. Ditlevsen (1914: 1150; possibly an erroneous record taken from Odhner, 1905: 354).

—— [stomach] Loch Craiglin, Argyll, Scotland. Raymont (1952: 117).

—— [?] Den Helder, Holland (Mar., 1961). Willemse (1968: 85; as *Hemiurus appendiculatus*).

—— [stomach] Airds Bay, Loch Etive, Argyll, Scotland. Dartnall & Walkey (1979: 472).

Leptoclinus maculatus [?] Greenland. Odhner (1905: 353).

Limanda limanda [stomach] West coast of Sweden. Odhner (1905: 355+plate III).

—— [?] Western Kattegat and Øresund. Køie (1981: 61).

—— [stomach] Øresund, western Kattegat, Skagerrak, North Sea west of Helgoland, off west Jutland, off Egersund in Norway, off the Faeroes (depth 10–84 m). Køie (1983: 204).

Myoxocephalus scorpius [?] Scandinavia. Odhner (1905: 355).

(?) *Osmerus eperlanus* [?] Scandinavia. Odhner (1905: 355). (It is difficult to know whether this is an original record or a repeat of von Linstow's (1873) report of *Distoma tectum*, which is probably from the Baltic coast of Germany.)

—— [?] Wierbalg, Holland (Feb., 1964). Willemse (1968: 85; as *H. appendiculatus*).

Platichthys flesus [?] Walney Channel, Barrow-in-Furness, Cumbria, England. Markowski (1966: 192; as *H. communis*; specimens in BM(NH) collection are *B. crenatus*).

Pleuronectes platessa [stomach] Roscoff, Finistère, France (June, 1937). Sproston (1939: 39).

Salmo salar [oesophagus] Verberg, Sweden (Aug.). Olsson (1868: 48; as *Distoma ocreatum*; see Odhner, 1905: 352).

—— [gut] River Rhine at Basle, Switzerland. Zschokke (1896: 776; as *Distomum appendiculatum* and *D. ocreatum*); (June) Hausmann (1897: 22; as *D. appendiculatum* and *D. ocreatum*). (See Heitz, 1918: 343).

—— [oesophagus, stomach] River Rhine, West Germany. Heitz (1918: 343; 1919: 510).

—— [?] River Elbe, West Germay. Fritsch (1894: 110; as *Distoma appendiculatum*). (See Heitz, 1918: 344).

(?) —— [stomach] Belgian coast. van Beneden (1871: 69; as *Distoma ocreatum*).

(?) —— [?] Greenland. Ditlevsen (1914: 1150) [Probably an erroneous record taken from Odhner, 1905: 354.]

—— [?] West coast of Sweden. Odhner (1905: 354).

—— [?] River Exe, Devon, England. Kennedy (1975: 66).

Salmo trutta [?] West coast of Sweden. Odhner (1905: 355+pl. III).

—— [?] t'Horntje, Texel, Holland (Apr., 1961). Willemse (1968: 84; as *H. appendiculatus*).

Spinachia spinachia [stomach] Airds Bay, Loch Etive, Argyll, Scotland. Dartnall & Walkey (1979: 472).

Aspect of biology. The life-history of this parasite is not known for certain, although Reimer (1971) has described *Cercaria caudofilamentosa*, from *Rissoa membranacea* in the Baltic, and suggested that it might be a larval form of this species. Køie (1983), who also recorded this cercaria, has supposed that other rissoid species may be hosts in other parts of this parasite's extensive range. Metacercariae have been recorded in *Acartia* sp. in the Baltic (Reimer, 1971), in *Sagitta elegans* in the White Sea (Kulachkova, 1972*a*) and in *Pleurobrachia pileus* from the northern Øresund (Køie, 1983). (Yamaguti (1975: plate 38) and Køie (1983) list Linton's (1927) record of 'distomes' from *Sagitta elegans* off New England as being *B. crenatus*; but, in our opinion, Linton's description indicates that these specimens are much more likely to have been *Hemiurus levinseni*.) The life-history appears, therefore, somewhat similar to that of *Hemiurus* spp. It is likely that there are other records of this species in chaetognaths or copepods, but that they have been confused with *Hemiurus* spp. and recorded under names such as *Distoma appendiculatum*. With such second intermediate hosts it would appear that, as far as the wide range of larger non-clupeid hosts is concerned, small fishes, such as sand-eels, must act as obligatory third intermediate hosts. Nothing is known about the seasonal prevalence of this

worm, except that Kulachkova (1972), who examined chaetognaths between May and October, noted that the prevalence in the White Sea was highest during September and October.

Mamaev & Oshmarin (1963) who studied the distribution of this species, indicated that, although it was found in situations varying from freshwater to oceanic, its procreation occurred in coastal waters. Its prevalence in waters on the continental shelves is very apparent when its distribution is studied. Its range appears to be restricted to the northern hemisphere, although Gaevskaja & Rodjuk (1983) claim to have found it in a nototheniid and a macrourid off the Falkland Islands, and almost entirely north of 30°N. Its distribution is, therefore, probably arctic-boreal, but probably not circum-polar (Gibson & Valtonen, 1981; Gibson, 1982, 1983), for, although it occurs in Arctic waters of the Barents and Kara Seas, there are no records in Canadian or Siberian Arctic waters. As in the case of *Hemiurus levinseni,* which has a similar arctic-boreal distribution, its range appears to extend more southerly on the western sides of the Atlantic and Pacific Oceans, i.e. to Florida and Japan, respectively. On the eastern sides of these oceans it extends southerly only to about 50°N, i.e. to the northern Bay of Biscay and Puget Sound, although the situation in the Atlantic region is complicated by anomalous and, therefore, questionable records of this species from the northern Mediterranean and the Black Seas.

Margolis (1963) and Pippy (1980) mentioned this species when attempting to use parasites as biological indicators of salmon populations, but the fact that it is a marine parasite and that little is known of its biology precluded its use in these instances. Nevertheless, the presence of *B. crenatus* is characteristic of recent anadromous migration into freshwater in salmon (Kennedy, 1975) and char (Dick & Belosevic, 1981). It is known to occur deep into freshwater in salmon on their spawning migration, for example, in the Rhine (prior to its pollution) as far as Switzerland (see above) and at the northern end of the Gulf of Bothnia (Valtonen *et al.,* 1984).

Previous descriptions. Lander (1904: 1; as *Hemiurus crenatus*; very detailed); Odhner (1905: 352); Nicoll (1907: 88; no figures); Looss (1908: 157); Lühe (1909: 138); Babaskin (1928: 213; as *B. amuriensis*); Yamaguti (1934: 443); Lloyd (1938: 117); Slusarski (1958: 399); Zhukov (1960: 40); Reimer (1970: 81).

Description (Figs 23, 24). This description is based upon 14 whole-mounted specimens, many of which are in poor condition, and three serially sectioned specimens. The body of this usually small worm (Table 13) is tubular to slightly spindle-shaped, its length depending upon the extent to which the *ecsoma* is everted. The latter organ may be completely withdrawn or protrude a distance of up to two-thirds the length of the soma (or almost the length of the soma according to the literature). As in the case of *Hemiurus communis,* a double invagination of the ecsoma often occurs. Much of the body-surface is covered with distinct transverse, annular *plications.* These are absent on the ecsoma and ventrally between the suckers, although fine ridges do appear in the latter position. As in poorly preserved material of other hemiurids, the presence of circular muscle-bands can cause small annular elevations on the ecsoma (cf. *Hemiurus* spp.). The plications also die out posteriorly on the ventral surface usually at a level roughly half-way between the vitellarium and the posterior extremity of the soma, laterally at about the level of the vitellarium and dorsally at about the level of the ovary or just anterior to it. They are much closer together in the anterior part of the body, and differ from those in *Hemiurus* spp. in that they are slightly crenulate. Mid-ventrally in the posterior half of the forebody there is a distinct presomatic pit (Fig. 24A). The aperture is usually a rounded subtriangular shape, but varies from being oval to a transverse slit. In contracted forms it may appear superficially to be extended laterally as a ventro-cervical groove. Internally the pit is lined by a thick layer of granular material, which is thicker and more extensive on the antero-lateral walls. It is not clear whether this material is glandular or muscular; but similar material (Fig. 24A) also occurs ventrally in the forebody both anteriorly and posteriorly to the genital pore (see Lander, 1904; Lloyd, 1938). We observed no sign of a papilla at the base of this pit (cf. Lloyd, 1938).

The *oral sucker* is ventrally subterminal and surmounted by a small, and usually indistinct, pre-oral lobe, which appears to bear a pair of small, protrusible papillae (see fig. 1 of Lander, 1904). The *ventral sucker,* which is similar in size or slightly larger than the oral sucker, is

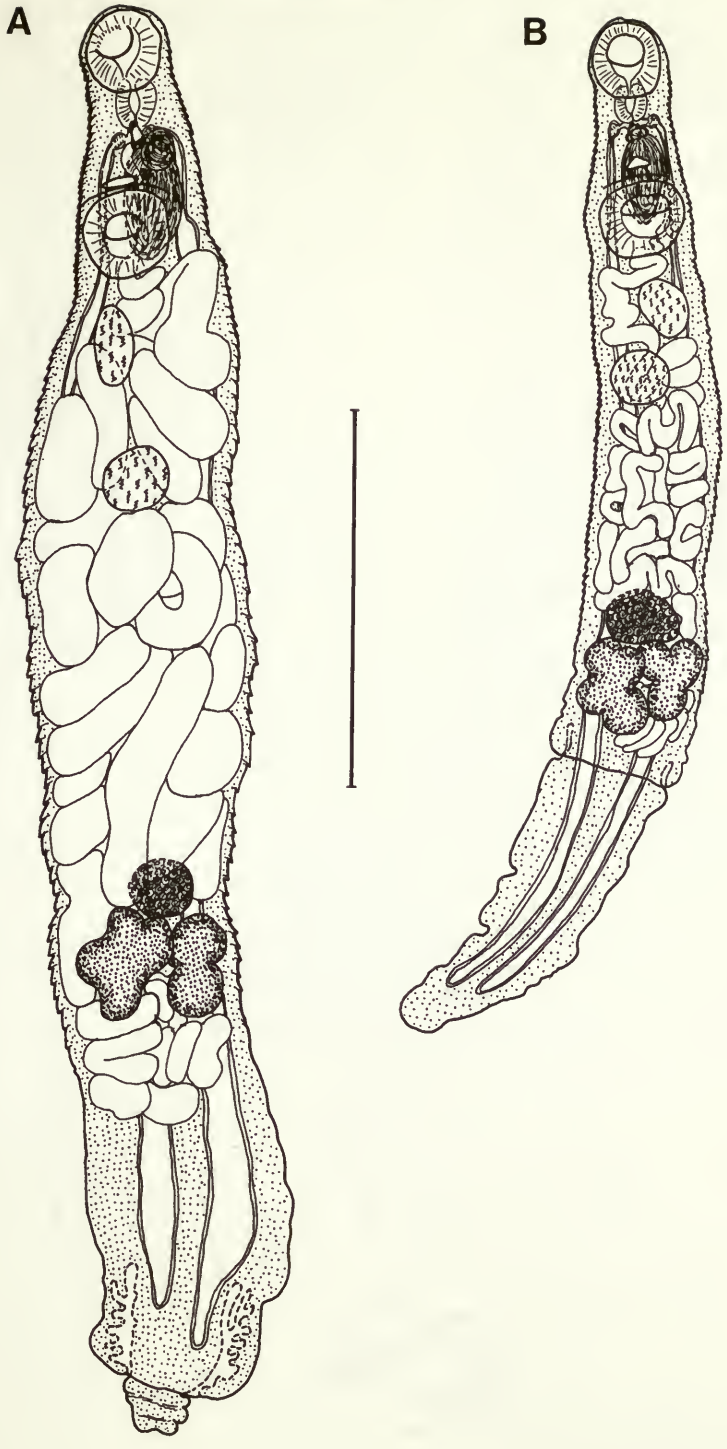

Fig. 23 *Brachyphallus crenatus*. (A) Entire worm, ex *Hippoglossus hippoglossus* off eastern Canada; (B) Entire worm, ex *Reinhardtius hippoglossoides* off eastern Canada. Scale bar: 1 mm.

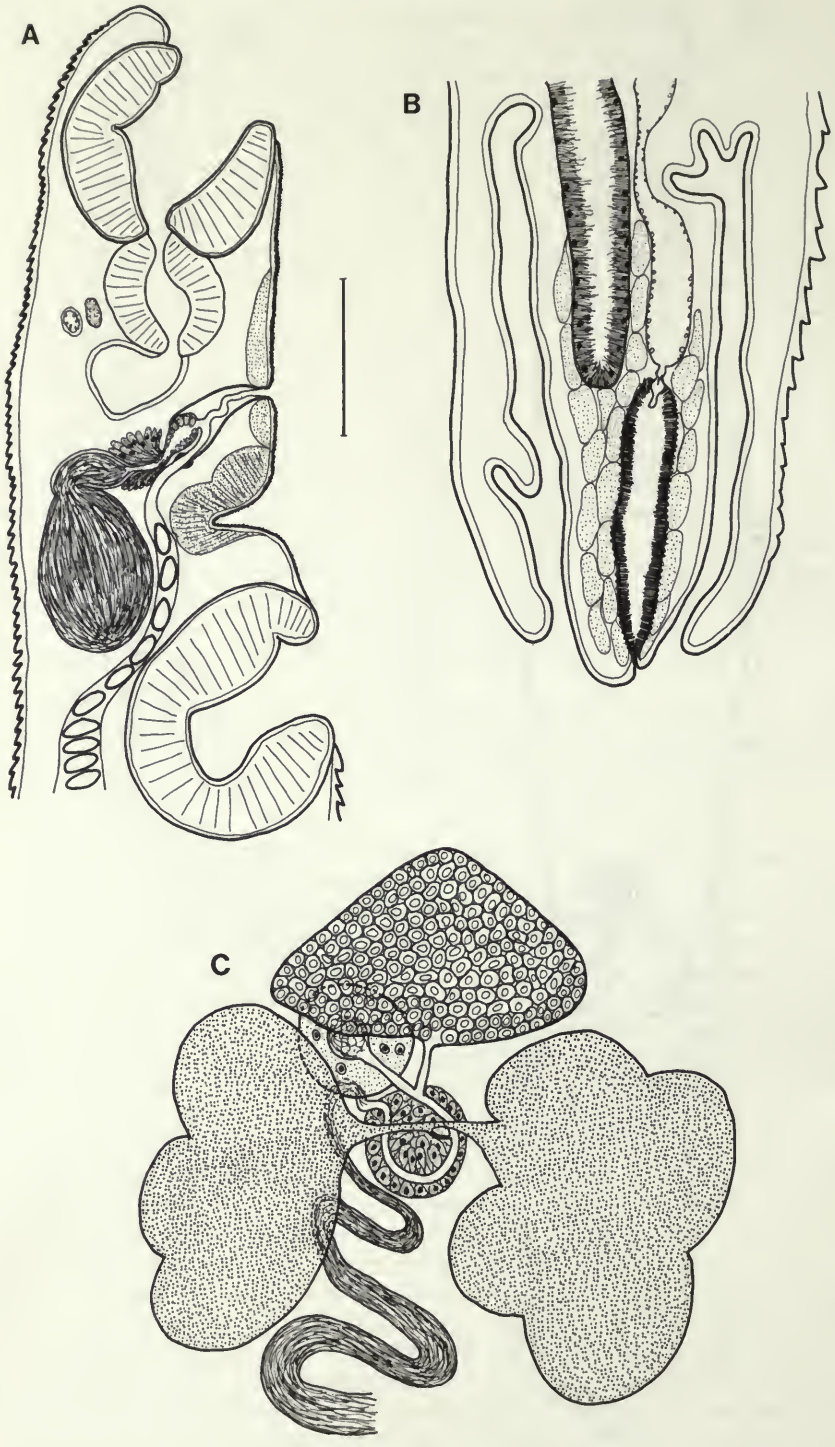

Fig. 24 *Brachyphallus crenatus*. (A,B) Sagittal section of forebody (A) and ecsoma (B), ex *Salmo salar*, Kaliningrad (material of A. Looss); (C) Diagram of ovarian complex, slightly exploded and modified after Lander (1904). Scale bar: A,B 300 μm.

Table 13 Measurements of *Brachyphallus crenatus*

Authority	Lander (1904)	Zhukov (1960)	Reimer (1970)	Present material
Host	*Anguilla rostrata*, *Osmerus mordax*	*Oncorhynchus gorbuscha*, *Hypomesus olidus*	Various	Various
Locality	East coast of USA	Sea of Okhotsk	Baltic Sea	North Atlantic
Length (mm)	1·71–3·22	1·24–2·5	0·58–1·74	0·85–3·75
Breadth (mm)	0·22–0·44	0·2–0·6	0·14–0·4	0·17–0·6
Ecsoma (mm)	average 0·8	0·31–0·78	0–1·05	0–1·3
Forebody (mm)	–	–	–	0·2–0·5
Oral sucker (mm)	0·22 average diam.	0·14–0·21 × 0·15–0·25	0·07–0·2 × 0·07–0·19	0·1–0·22 × 0·11–0·23
Ventral sucker (mm)	0·26 average diam.	0·15–0·22 × 0·17–0·26	0·08–0·19 × 0·08–0·19	0·11–0·23 × 0·14–0·26
Sucker-ratio	(1 : 1·2)	(1 : 1·1)	(1 : 1–1·2)	1 : 1–1·3
Testes (mm)	0·15 × 0·13 average	0·09–0·2 × 0·12–0·31	0·07–0·16 × 0·07–0·19	0·07–0·16 × 0·08–0·18
Ovary (mm)	0·11 × 0·16 average	0·08–0·17 × 0·12–0·25	0·05–0·12 × 0·07–0·17	0·06–0·17 × 0·08–0·19
Vitelline masses (mm)	0·2 × 0·11 average	–	0·09–0·19 × ?	0·1–0·4 × 0·08–0·3
Eggs (μm)	–	22–27 × 12–16	20–26 × 9–13	22–26 × 11–15

Figures in parentheses are calculated from measurements in the literature.

normally situated well within the anterior third of the soma, but it may be further back in the smallest specimens. Allometric growth is involved with this feature, as the length of the forebody in our material varies from 32 % of the soma in the smallest specimens to only 13 % in the largest.

There is no prepharynx. The muscular and globular *pharynx* gives rise posteriorly to an oval oesophagus, which is slightly smaller than the pharynx and is occasionally collapsed in fixed specimens. The oesophagus is oriented postero-dorsally and opens via a muscular sphincter into the middle of a short, narrow, transverse duct which almost immediately opens laterally to form the 'Drüsenmagen'. From these two organs, which are symmetrically situated postero-laterally and slightly dorsally to the pharynx, the caeca pass back in the dorso-lateral fields to end blindly deep within the ecsoma. The densely packed, villous lining of the caeca is much thicker in the distal (posterior) regions of the caeca.

The excretory pore is situated ventro-subterminally on the ecsoma. It opens into what appears to be a modified region of the *excretory vesicle*, which possesses a dense, villous lining. This region is elongate spindle-shaped and extends up to half the length of the ecsoma (Fig. 24B). It is connected to the remainder of the stem, which has a more typical structure, by what appears to be a valve. The tubular region of the stem passes anteriorly in the medial plane and bifurcates just posteriorly to the ventral sucker. The arms pass into the forebody in the dorso-lateral fields and unite dorsally to the pharynx.

The two oval *testes* normally occur obliquely to almost tandem a short, but distinct, distance posterior to the ventral sucker and in the ventral to ventro-lateral field. They are separated from each other by a short distance, which in larger specimens, may be equivalent to their own diameter. In contracted specimens the testes may occur obliquely to symmetrically, close together and adjacent to the posterior margin of the ventral sucker. The vasa efferentia appear to unite at the base of the seminal vesicle, but this is not very clear in our sections. The seminal vesicle is bipartite and extends back to the level of the ventral sucker, usually to about the middle of this

organ. The proximal part is large, oval to elongate-oval and possesses a thin wall, whereas the distal part is much smaller, usually tear-shaped and has a thicker, more muscular wall (Fig. 24A). In some specimens the distal part may be collapsed to form a fusiform or even tubular structure. The constriction between the two parts of the seminal vesicle tends to be antero-dorsal, with the result that the distal part appears to curve antero-ventrally. This latter part tapers into an unmodified duct of variable length which links it with the very short, tubular pars prostatica. This is surrounded by a relatively small number of gland-cells and is lined by a small number of anuclear blebs. In one set of sections there is an indication that there are two types of gland-cells surrounding the pars prostatica, as in *Lecithochirium fusiforme*; but it is not clear whether the larger cells are associated with the ejaculatory vesicle or the pars prostatica. Distally the pars prostatica opens into a glandular *ejaculatory vesicle* (prostatic vesicle) (Fig. 24A), which is situated just within the base of the sinus-sac. This vesicle is lined by a dense layer of anuclear blebs which protrude deep into the lumen. Distally it unites with the metraterm to form a narrow, often sinuous, tubular hermaphroditic duct, which opens directly through the genital pore mid-ventrally in the forebody at about the level of the posterior margin of the pharynx. There is no permanent sinus-organ and no genital atrium. The thin-walled *sinus-sac* is claviform and relatively small. Although the aperture at its base is wide, it is not really of the 'open'-type, as it appears to be closely applied to the surface of the metraterm and the ejaculatory vesicle (Fig. 24A).

The transversely oval *ovary* is usually situated ventro-medially (Fig. 23B), although it may be displaced to one side by the uterus in larger specimens (Fig. 23A). It occurs immediately anterior or antero-dorsal to the vitelline masses and is usually in the middle third of the hindbody (including ecsoma). It is separated from the testes by the bulk of the uterus. The short oviduct leaves the ovary posteriorly, passes postero-dorsally and is joined by the duct from Juel's organ. The latter organ is very distinct and situated postero-dorsally to the ovary. The oviduct then almost immediately penetrates Mehlis' gland, whereupon it receives the very narrow common vitelline duct (Fig. 24C). Within Mehlis' gland, which is situated mid-dorsally to the vitelline masses, the oviduct curves anteriorly; and, once it emerges, the first coils of the *uterus* occur immediately posterior to Mehlis' gland. These coils of the uterus form a uterine seminal receptacle, but this is often difficult to distinguish. The uterus loops posteriorly to the vitellarium to varying degrees, but normally the post-vitelline field is small and occasionally almost non-existent. It then passes anteriorly, coiling dorsal to and, in large specimens, lateral to the ovary. The bulk of the uterus fills the gap between the ovary and the testes. Further anteriorly the coils tend to loop around and between the two testes in a sigmoid configuration (Fig. 23). Dorsal to the ventral sucker the uterus narrows to form the metraterm, the proximal limit of which is indistinct. The metraterm passes directly forward ventral to the seminal vesicle and, as it enters the sinus-sac, it is surrounded by a sphincter. Within the sinus-sac the two ducts unite to form the hermaphroditic duct (Fig. 24A). The uterus contains numerous, small, oval and operculate eggs. The *vitellarium* is composed of two large, lobed masses which occur symmetrically in the ventral or subventral field immediately posterior to the ovary. The lobes are short and broad, normally being greater in breadth than length. They are usually quite distinct, but may be obscured when viewed from the side. There are normally four lobes on one mass and three on the other. The masses give rise medially to short, transverse vitelline ducts, which unite medially to form a narrow common duct, which opens into the oviduct within Mehlis' gland (Fig. 24C).

Discussion. The systematics of this species is more straightforward than is the case for many other hemiurids. Looss (1908) erected *Brachyphallus affinis* for the American form of this species described by Lander (1904), and Babaskin (1928) erected *B. amuriensis* for the form from the Pacific coast of Siberia. Although no later workers appear to have accepted the validity of *B. affinis*, which was discussed by Manter (1926), *B. amuriensis* was accepted by Soviet workers until the work of Zhukov (1960). It is worth mentioning, however, that there may have been considerable confusion between *B. crenatus* and *Hemiurus luehei* in salmonids by workers in the latter part of the 19th century, and it is possible that there has been some confusion between *B. crenatus* and *Lecithochirium* spp. in the northern Mediterranean and Black Seas.

Two obvious features of interest are the well-developed presomatic pit and the modification of the distal region of the stem of the excretory vesicle. The function of these features is not known. It seems likely, however, that Lloyd's (1938) suggestion, that the presomatic pit may be involved with the detection of chemical changes in the environment associated with the retraction and protrusion of the ecsoma, is somewhat implausible, considering the absence of this organ in the majority of hemiurids. With regard to the excretory vesicle, the villous lining of the distal region, and the fact that it is separated from the remainder of the vesicle by a valve, suggest that it may be involved in the selective reabsorbtion of ions in the 'excretory' fluid. Whether or not this is associated with the prevalence of this species in migratory salmonids which penetrate deeply into freshwater has yet to be ascertained.

Subfamily **PLERURINAE** Gibson & Bray, 1979

DIAGNOSTIC FEATURES. Body small; spindle-shaped to cylindrical. Ecsoma reduced or well developed. Body-surface smooth, or occasionally with crenulate plications giving a scaly appearance. Presomatic pit absent, except in *Synaptobothrium*. Testes symmetrical to tandem; usually oblique. Seminal vesicle elongate, saccular and constricted into two, three or four sections; thin-walled, although certain sections may have thicker walls; in forebody to partly in hindbody. Pars prostatica vesicular or tubular; may be partly enclosed by muscles of sinus-sac; commonly linked to seminal vesicle by aglandular duct. Sinus-sac apparently absent or poorly developed; when present usually of 'open'-type. Permanent sinus-organ absent. Ejaculatory (prostatic) vesicle absent. Hermaphroditic duct commonly vesicular proximally and tubular distally. Genital atrium usually deep, but may be shallow or apparently absent. Ovary entire or lobed. Vitellarium composed of two quadri- and tri-lobed masses; lobes small to digitiform. Excretory arms united in forebody. Parasitic in stomach of marine teleosts.

Key to plerurine genera occurring in the north-east Atlantic

1 Seminal vesicle in forebody; presomatic pit present; body-surface smooth . . . . . *Synaptobothrium* (p. 103)

– Seminal vesicle at least partly extended into hindbody; presomatic pit absent; at least part of body-surface with crenulate plications ('scales') . . . . . *Dinosoma* (p. 97)

Genus *DINOSOMA* Manter, 1934

DIAGNOSTIC FEATURES. Body-surface with crenulate plications, giving 'scaly' appearance. Testes symmetrical to tandem. Seminal vesicle postero-dorsal to ventral sucker; saccular, bipartite or wide; sinuous. Pars prostatica vesicular; may be connected to seminal vesicle by long, aglandular duct. Sinus-sac apparently absent. Hermaphroditic duct long, narrow; with small vesicle proximally. Ovary oval. Vitellarium two indented or lobed masses.

TYPE-SPECIES. *Dinosoma rubrum* Manter, 1934 [by original designation].

Dinosoma ventrovesicularis sp. nov.

TYPE-HOST AND LOCALITY. *Xenodermichthys socialis*, Porcupine Bank (54°N, 14°W) off western Ireland.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Xenodermichthys socialis [stomach] Porcupine Bank (54°N, 14°W; depth 1,050 m; June, 1974). BM(NH) 1984.9.20.6. (Holotype).

(b) From elsewhere
None.

(ii) NE Atlantic records from the literature
Xenodermichthys socialis [?] Off Scotland. Campbell (1983: 521).

ASPECTS OF BIOLOGY. Virtually nothing is known about the biology of this species, except that, like many of its congeners, it would appear to be a deep-water form. Campbell (1983) identified the hemiurid found by Markle & Werner (1979) in *Xenodermichthys copei* (=*socialis*) as *Dinosoma* sp. It had originally been considered *Lethadena* or *Dinosoma* and was found in 14 % of *X. copei* from the bottom and in 4·5 % from midwater off the eastern coast of the USA. Campbell's brief reference to a *Dinosoma* sp. from *'X. copei'* off Scotland refers to the present specimen.

PREVIOUS DESCRIPTIONS. None.

DESCRIPTION (Figs 25, 26). This description is based upon one specimen, measuring 2·0 mm in length by 0·45 mm in maximum breadth, which was initially studied as a whole-mount and then unmounted and serially sectioned. The body of the worm is elongate and spindle-shaped (Fig. 25). The withdrawn *ecsoma* of this specimen is well developed. The body-surface is smooth, except for a region of crenulate *plications* ('scales') (Fig. 25C) on the ventral surface immediately posterior and lateral to the ventral sucker, extending slightly further anteriorly and posteriorly in the lateral fields such that it reaches forward just into the forebody and backwards about halfway to the ovary. There is also an indistinct area of 'scales' dorsal to the oral sucker (Fig. 26). They are especially distinct around the posterior margin of the ventral sucker. There is no presomatic pit. The *oral sucker* (0·17 × 0·17 mm) is ventrally subterminal, being surmounted by a narrow pre-oral lobe which bears a small, submedian, terminal projection (Fig. 25A) and several papillae. The oral sucker is about half the width of the large, well-developed *ventral sucker* (0·35 × 0·34 mm), most of which is inside the anterior third of the body. The forebody measures 0·42 mm.

There is no prepharynx, but the well-developed *pharynx* (0·1 × 0·1 mm) opens posteriorly into a small, globular oesophagus of only about half the size of the pharynx itself. The oesophagus opens postero-dorsally via a sphincter (Fig. 26) into a short, transverse commissure which dilates on both sides as it passes laterally and opens into well-developed 'Drüsenmagen'. These, in turn, open posteriorly into the caeca, which pass back into the dorso-lateral fields and end blindly close to the base of the withdrawn ecsoma.

The excretory system is very unusual. The pore, which occurs ventro-terminally on the ecsoma, leads into a Y-shaped *excretory vesicle*. The initial part of the stem is tubular and narrow; but just after passing into the soma it narrows suddenly and is connected to the remainder of the stem by a sphincter or valve (presumably, when the ecsoma is everted, this partition would be within the ecsoma (?) or even form part of the external wall of the ecsoma) (Fig. 25B). In this specimen the first part of the remainder of the stem is relatively wide and coiled just posterior to the post-vitelline coils of the uterus. It then runs forward sinuously in the lateral field past the ovarian complex on the opposite side of the body to the ovary (Fig. 25A). Next it loops across the body ventrally just anterior to the ovary and is coiled, in both the ventral field (Fig. 25A,B) and the lateral field on the opposite side of the body to the ovary, between the ovary and the testes. Between the testes it passes directly anteriorly in the ventral field and bifurcates close to the posterior margin of the ventral sucker. The much narrower arms pass dorso-laterally to the ventral sucker, ventro-laterally in the forebody (ventral to the caeca) and then dorso-laterally at the level of the pharynx. They unite dorsally to the pharynx. Another interesting feature of this excretory system is that in the more distal regions the excretory corpuscles are much more refractive than they are in the proximal regions, such that the posterior half of the system is very easily seen.

The two oval, slightly oblique *testes* (0·12 × 0·10 and 0·11 × 0·09 mm) occur close to the posterior margin of the ventral sucker and are widely separated by the coils of the uterus and by the excretory vesicle. The testis on the ovarian side of the body is slightly more posterior and in the ventro-lateral field, whereas the other occurs in the lateral field. Two short, stout vasa efferentia leave the testes, pass medially and appear to unite as they enter the base of the seminal vesicle. The latter organ is elongate-saccular, being situated in this specimen almost entirely between the anterior and posterior margins of the ventral sucker, although, because it curves around the

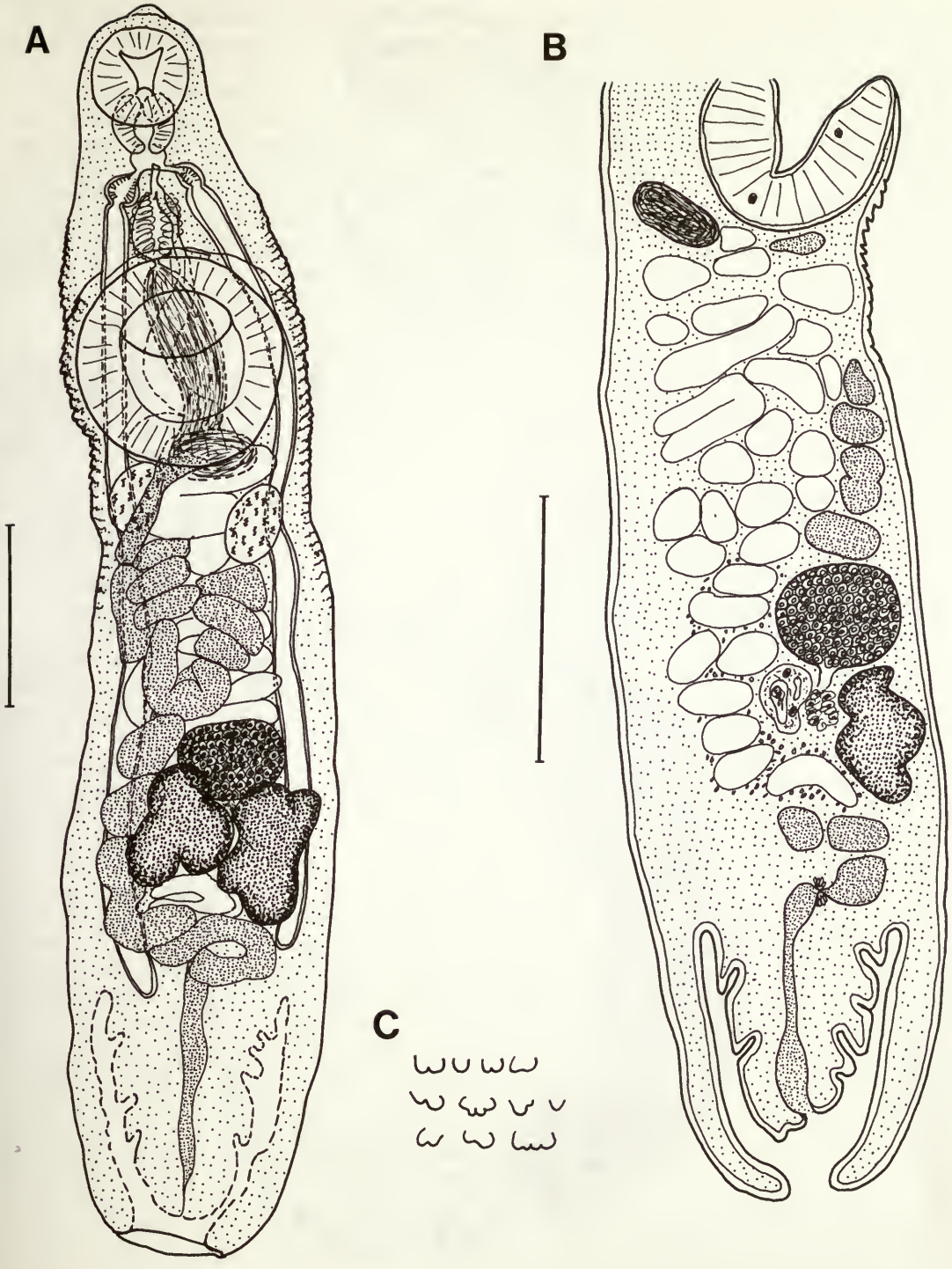

Fig. 25 *Dinosoma ventrovesicularis* sp. nov. ex *Xenodermichthys socialis*. (A) Entire worm; (B) Sagittal section of hindbody, showing the unusual course of the excretory vesicle; (C) Crenulate plications ('scales'). Scale bars: A,B 300 μm. (Excretory system stippled).

Fig. 26 *Dinosoma ventrovesicularis* sp. nov. Sagittal section of forebody. Scale bar: 100 μm.

dorsal surface of the sucker, it is in fact longer than the sucker. There is an indication that the posterior third of the seminal vesicle is constricted as it curves ventrally under the postero-dorsal surface of the ventral sucker (Fig. 26). The wall of this organ is thin but distinct. Distally it unites with the pars prostatica via a narrow, coiled, aglandular duct. (In our observations of *D. rubrum* it would appear that this duct is either very elastic or may form part of the seminal vesicle when the latter is swollen with spermatozoa, as the distance between the seminal vesicle and the pars prostatica in this species is very variable.) The pars prostatica is vesicular, quite large, lined with anuclear blebs and closely invested by a single layer of gland-cells with very short ducts (Fig. 26). It occurs medially and intercaecally in the posterior half of the forebody. In this specimen it is slightly dorso-ventrally flattened, but this may be an artifact resulting from the fact that the sections were cut from a demounted whole-mount. Distally the pars prostatica opens into a short, narrow ejaculatory duct which passes ventrally and unites with the metraterm to form the hermaphroditic duct. There is no sign of a *sinus-sac*. The proximal region of the hermaphroditic duct is short and narrow, but this soon opens out to form what appears to be a hermaphroditic vesicle, which apparently has a tegumental lining and is surrounded by small gland-cells (Fig. 26). As there is only one specimen we cannot be certain that this is a consistent feature or merely a particular condition of the contraction of the duct, which in other species appears to be very elastic. One reason to doubt the presence of a hermaphroditic vesicle is that it is difficult to imagine how one could function in the absence of a sinus-sac. The distal region of the hermaphroditic duct is narrower, passes ventrally and opens through the genital pore mid-ventrally at the level of the posterior margin of the pharynx. There appears to be no genital atrium, although it is possible that part of the hermaphroditic duct might have originated from this structure.

The transversely oval *ovary* (0·13 × 0·18 mm) occurs in a ventrally submedian position towards the left side of the body. It is within the posterior half of the soma, well posterior to the testes and separated from them by coils of the excretory vesicle and the uterus. The short oviduct leaves the ovary posteriorly and enters Mehlis' gland, which is sandwiched between Juel's organ dorsally and the vitellarium ventrally (Fig. 25B). Although it is not clear in our sections, shortly before or after entering Mehlis' gland the oviduct must receive the duct from Juel's organ and the common vitelline duct, respectively. Within Mehlis' gland the oviduct passes posteriorly and then curves to run antero-dorsally. Upon leaving Mehlis' gland it dilates to form the uterus and again passes posteriorly. Few spermatozoa were seen in the proximal region of the *uterus*, as it was full of eggs, but presumably a uterine seminal receptacle is normally present. There are a small number of uterine coils posterior to the level of the vitellarium. It then loops forward dorsally to the ovarian complex (Fig. 25B): this unusual position is presumably caused by the unusual extent of the excretory vesicle. The remainder of the uterine coils occur mainly dorsal to the excretory vesicle between the ovary and the ventral sucker, although they tend to be pushed more towards the ovarian side of the body by the lateral coils of the excretory vesicle on the other side. The uterus, therefore, reaches close to the ventral surface of the body only laterally on the ovarian side of the body and between the testes. Ventrally to the posterior region of the seminal vesicle the uterus narrows and passes forward at first sinuously and then directly, gradually becoming even narrower. There is no distinct transition into a metraterm, but ventrally to the pars prostatica the uterus is reduced in this specimen to a narrow duct. Ventrally to the anterior extremity of the pars prostatica, immediately beyond a small sphincter (Fig. 26), it receives the ejaculatory duct dorsally and continues as the hermaphroditic duct. The uterus contains numerous, small, oval and operculate eggs (17–22 × 12–15 μm; usually 19–21 × 13–14 μm). The *vitellarium* is composed of two distinctly lobed masses, the lobes being roughly as long as they are wide. There are three such lobes on one mass and four on the other (Fig. 25A). The masses are juxtaposed symmetrically in the ventral field, submedially and immediately posterior to the ovary. Dorso-medially they give rise to two very short, stout vitelline ducts, which appear to unite to form a short, narrow common duct. This, in turn, presumably unites with the oviduct within Mehlis' gland; but this was not clear in our sections.

Discussion. The literature on the genus *Dinosoma* Manter, 1934, indicates that the genus is in

need of critical study. Little is known of the intra-specific variation occurring in: (1) the shape of the vitellarium; (2) the distribution of the 'scales' (it is possible that some confusion with *Adinosoma* Manter, 1947, has occurred: it is worth noting that Zubchenko (1978) described *A. gaevskaye* from *Conger conger* off the Azores to the south of our region); (3) the shape of the seminal vesicle; (4) egg-size; (5) body-size; and many other features. At the present time such a study is not possible, as, with the exception of *D. tortum* Yamaguti, 1938, and single extra records of *D. rubrum* Manter, 1934, by Bravo Hollis & Caballero Deloya (1973) and *D. triangulata* Campbell & Munroe, 1977, by Gaevskaja & Aleshkina (1983), all of the species of this genus have been reported only once.

It is very evident that the course of the excretory vesicle in the present specimen is significantly different from all previous descriptions of *Dinosoma* spp., although, to be fair, it must be stated that in no case has the excretory vesicle been described in detail, but a typical hemiurid arrangement is often intimated. The peculiar shape and position of this organ in our specimen was so obvious that, if present in other species, it would seem unlikely to have been overlooked. Nevertheless, we have examined Manter's sections of *D. rubrum*, and it does appear that in this, the type-species of the genus, this vesicle is also unusual and extends into the ventral field between the ovary and the ventral sucker, although not to the same extent as in our specimen. Similarly, we have examined some specimens from *Lophius piscatorius* from off the coast of Morocco which resemble *D. rubrum*, although they are in too poor a condition for us to be sure. In this material the arrangement of the excretory vesicle appears to resemble that of Manter's material. It is possible, therefore, that an anomalous excretory vesicle is a feature of many or indeed all members of the genus, although its omission from descriptions tend to suggest otherwise.

Our specimen can be distinguished from most members of the genus by egg-size. Yamaguti's (1938) species *D. apogonis, D. hynnodi, D. manteri* and *D. synaphobranchi* all have much larger eggs, usually being in the region of 30 μm or more in length: the latter species are morphologically somewhat similar and may prove to be synonymous. In addition, *D. rubrum, D. tortum* Yamaguti, 1938, *D. oregonensis* McCauley & Pequegnat, 1968, *D. pectoralis* McCauley & Pequegnat, 1968, *D. lophiomi* Toman, 1973, *D. triangulata* Campbell & Munro, 1977, *D. zeusi* Parukhin, 1978, and *D. aguljasi* Tkachuk, 1979, all have slightly larger eggs (normally in the region of 23–29 μm). Only *D. sulca* Campbell & Munro, 1977, and *D. polymixiae* Yamaguti, 1970, were reported to have eggs in the same range as our specimen, although our measurements of a paratype of the former indicate that the eggs are significantly larger (23–27 × 11–14 μm) than reported. *D. polymixiae*, an Hawaiian species, can be differentiated from our specimen by its smaller sucker-ratio.

Since the present specimen was taken from a bathypelagic fish, *Xenodermichthys socialis* (Alepocephalidae), and bathypelagic fishes normally possess a different digenean fauna to neritic species, it is really necessary to discuss further only the forms from bathypelagic fishes, i.e. *D. oregonensis, D. pectoralis, D. sulca* and *D. triangulata*, although it should not be forgotten that *D. lophiomi, D. aguljasi* and probably both *D. rubrum* and *D. polymixiae* occur in fishes which extend well into mesopelagic depths. *D. sulca*, known from species of *Antimora* (Moridae) and *Alepocephalus* (Alepocephalidae) from the Hudson Canyon, NW Atlantic, is much larger than our specimen and has a smaller pars prostatica with a more extensive covering of gland-cells, a more elongate and coiled seminal vesicle and a longitudinal ventral groove in the anterior hindbody. *D. triangulata* is recorded from the same hosts and locality as *D. sulca* and also from the same species of *Antimora* off Guinea-Bissau (Gaevskaja & Aleshkina, 1983). In addition to its larger eggs, it differs from the present specimen in several features, including having a totally different body-shape. Morphologically and metrically the closest relatives to our specimen appear to be *D. oregonensis* and *D. pectoralis*, both from macrourids, including *Chalinura* and *Coryphaenoides* (=*Hemimacrurus*), off Oregon. The latter two species are metrically very similar to each other and may prove to be synonymous. They differ from the specimen from *Xenodermichthys* in the shape of the seminal vesicle, which is claimed to be sinuous in one species and to have proximal, subspherical expansion in the other, in addition to possessing larger eggs.

In view of the fact that (1) we cannot relate the worm from *Xenodermichthys* to any known species of the genus, and especially to any species from bathypelagic fishes, and (2) the peculiar

form of the excretory vesicle in our specimen, we have considered it to represent a new species for which we have erected the name *D. ventrovesicularis* sp. nov.

Genus *SYNAPTOBOTHRIUM* von Linstow, 1904

DIAGNOSTIC FEATURES. Body-surface smooth. Presomatic pit present; circular or oval; deep; glandular. Testes oblique. Seminal vesicle bipartite (? or tripartite); anterior part small; posterior part long; thin-walled; occurring mostly in forebody, but may extend dorsal to ventral sucker. Pars prostatica tubular with wide lumen; may extend into base of sinus-sac. Sinus-sac weakly developed; of 'open'-type. Ovary oval. Vitellarium two lateral masses with three and four short lobes. Eggs may be reniform.

TYPE-SPECIES. *Synaptobothrium caudiporum* (Rudolphi, 1819) [syn. *S. copulans* von Linstow, 1904 – type by monotypy].

Synaptobothrium caudiporum (Rudolphi, 1819) Looss, 1907

Distoma caudiporum Rudolphi, 1819.
Lecithochirium caudiporum (Rudolphi) Lühe, 1901.
Synaptobothrium copulans von Linstow, 1904.
Lecithochirium copulans (von Linstow) Odhner, 1906.

TYPE-HOST AND LOCALITY. *Zeus faber*, off Rimini, Italy.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Pomatoschistus minutus [stomach] Blakeney Harbour, Norfolk, England (Jul., 1959). BM(NH) 1959.10.14.35.
Scophthalmus rhombus [stomach] Newhaven, Sussex, England (Oct., 1953). Collected by C. A. Wright. BM(NH) 1974.2.15.7–8.
—— [buccal cavity] Unknown (Oct., 1953). BM(NH) 1963.4.10.3–20.
Zeus faber [stomach] Off Portugal (40°N, 10°W; depth 78–88 m; Jan., 1971). BM(NH) 1984.1.12.9.

(b) From elsewhere
Zeus faber [stomach] Banyuls, Pyrenées Orientales, France (May, 1961). BM(NH) 1984.1.12.10.

(ii) NE Atlantic records from the literature

Adults from the gut

Arnoglossus laterna [gut] Louvain, Belgium. von Linstow (1904: 252; as *S. copulans*); Odhner (1906: 60; as *Lecithochirium copulans*).
Conger conger [stomach] Plymouth, Devon, England. Baylis & Jones (1933: 631); Baylis (1939: 483).
Gadus morhua [stomach] Plymouth, Devon, England. Dawes (1947: 292).
Lophius piscatorius [stomach] Plymouth, Devon, England. Nicoll (1914: 486); Dawes (1947: 292).
? —— [?] NE Atlantic. Gaevskaja (1978*a*: 83). Possibly not an original record.
Pleuronectes platessa [stomach] Plymouth, Devon, England. Dawes (1947: 292).
Scophthalmus rhombus [stomach] Galway, Eire. Little (1929: 26).
—— [stomach] Plymouth, Devon, England. Baylis & Jones (1933: 631); Baylis (1939: 483).
Trigla lucerna [stomach] Plymouth, Devon, England. Nicoll (1914: 486). (The record of Baylis & Jones (1933: 631) and Baylis (1939: 483) from this host is a misdetermination: the material in question appears to belong to the genus *Hemiurus*).
Trisopterus luscus [stomach] Plymouth, Devon, England. Dawes (1947: 292).
Zeus faber [intestine] Belgian coast. van Beneden (1871: 42; as *Distomum caudiporum*).
—— [stomach] Plymouth, Devon, England. Nicoll (1914: 486).
—— [stomach] Galway, Eire. Little (1929: 27).

Encapsulated form

It is very possible that these records may refer to lecithochiriines, such as *L. rufoviridae, L. furcolabiatum* or *L. musculus*.
(?) *Blennius pholis* [encapsulated in viscera] Plymouth, Devon, England. Nicoll (1915: 356).
(?) —— [encapsulated on peritoneum] Roscoff, Finistère, France (June, 1937). Sproston (1939: 41).

(?) *Labrus bergylta* [encapsulated in liver and intestinal wall] Plymouth, Devon, England. Nicoll (1914: 486).
(?) —— [encapsulated in intestine] Roscoff, Finistère, France (June, 1937). Sproston (1939: 43).
(?) *Symphodus melops* [encapsulated in intestinal wall] Plymouth, Devon, England. Nicoll (1914: 486).
(?) —— [encapsulated in body-cavity] Roscoff, Finistère, France (June, 1937). Sproston (1939: 44).
(?) *Taurulus bubalis* [encapsulated in mesentery] Roscoff, Finistère, France (June, 1937). Sproston (1939: 42).

Aspects of biology. Little is known about the biology of this species, but it is likely that its life-history is similar to that of the related lecithochiriines. Encapsulated, immature specimens claimed to be of this species have been reported from the gut-wall, mesentery and body-cavity of blenniid, labrid and cottid fishes by Nicoll (1914, 1915) and Sproston (1939); but the similarity between such forms and related lecithochiriine species (see above) suggests that these records require confirmation. Judging by the diet of the major definitive hosts of this species in our waters, i.e. *Scophthalmus rhombus, Arnoglossus laterna* and *Zeus faber,* it would appear that bottom-dwelling, small fishes, such as gobies, might act as intermediate hosts. Other hosts, for example, *Conger conger, Gadus morhua, Lophius piscatorius, Pleuronectes platessa, Trigla lucerna* and *Trisopterus luscus* are probably accidental hosts, although in some of these the parasite does apparently reach a very large size (Dawes, 1947). The possibility cannot, however, be dismissed that some of the records from the above hosts are the result of misdeterminations. Material from *Trigla lucerna* identified as *S. caudiporum* by Baylis & Jones (1933) and Baylis (1939) is in fact a species of *Hemiurus,* and material from *Platichthys flesus* in the Collection of the BM(NH) appears to be *Lecithochirium musculus.*

With regard to the distribution of this species, it occurs in coastal waters of the Mediterranean, Adriatic and Black Seas, and in the NE Atlantic region it has been recorded from off Portugal in the south to as far north as the southern North Sea. This Lusitanean distribution appears to match the range of the three main hosts listed above. Parukhin (1976*a*) claimed to have found this parasite in the Indian Ocean.

Previous descriptions. Lühe (1901*b*: 477; as *Lecithochirium caudiporum*; very brief, no figures); Odhner (1906: 60; as *Synaptobothrium copulans*; detailed); Looss (1908: 151; well-figured); Dawes (1947: 292); Dollfus (1953: 87; useful, but not original); Nikolaeva (1963: 409; measurements only; 1966: 58; measurements only); Kovaleva (1970*a*: 56; measurements only).

Description (Fig. 27). This description is based upon 12 whole-mounted and two sectioned specimens. This medium-sized hemiurid (Table 14) is spindle-shaped, tapering at both extremities, especially anteriorly. The *ecsoma* is withdrawn in all but one of our specimens: in fact it is usually so contracted that it is visible only as the thickened and convoluted wall of the ecsomal cavity (Fig. 27A). In one specimen it is slightly extruded, as in the figure of Looss (1908). One easily recognizable feature of this worm is that the opening of the ecsomal cavity is normally very wide (Fig. 27A,B): hence, presumably, the specific name! The surface of the body is smooth. Mid-ventrally just inside the posterior half of the forebody there is a distinct, oval presomatic pit. This pit is deep, surrounded by a thick, glandular layer (Fig. 27B). In some specimens it appears that a median papillate protrusion extends into the lumen of the pit. Between this pit and the ventral sucker there is often a transverse ventro-cervical groove, but its presence depends upon the state of contraction. The *oral sucker* is ventrally subterminal and surmounted by a small pre-oral lobe. The globular *ventral sucker,* which is situated at about one-fifth to one-quarter of the body-length from the anterior end, is usually slightly more than twice the size of the oral sucker.

There is no prepharynx, but the well-developed, oval *pharynx* is normally more than half the size of the oral sucker. The pharynx opens posteriorly into a short, wide and muscular oesophagus. This, in turn, opens posteriorly into two narrow, muscular ducts which pass laterally, forming the proximal region of the caeca. These ducts open, in the 'shoulder'-region, into the 'Drüsenmagen'. The remainder of each caecum passes back in the dorso-lateral field and ends blindly close to the base of the ecsomal cavity (Fig. 27A): it is possible that when the ecsoma is extended the caeca extend into this organ.

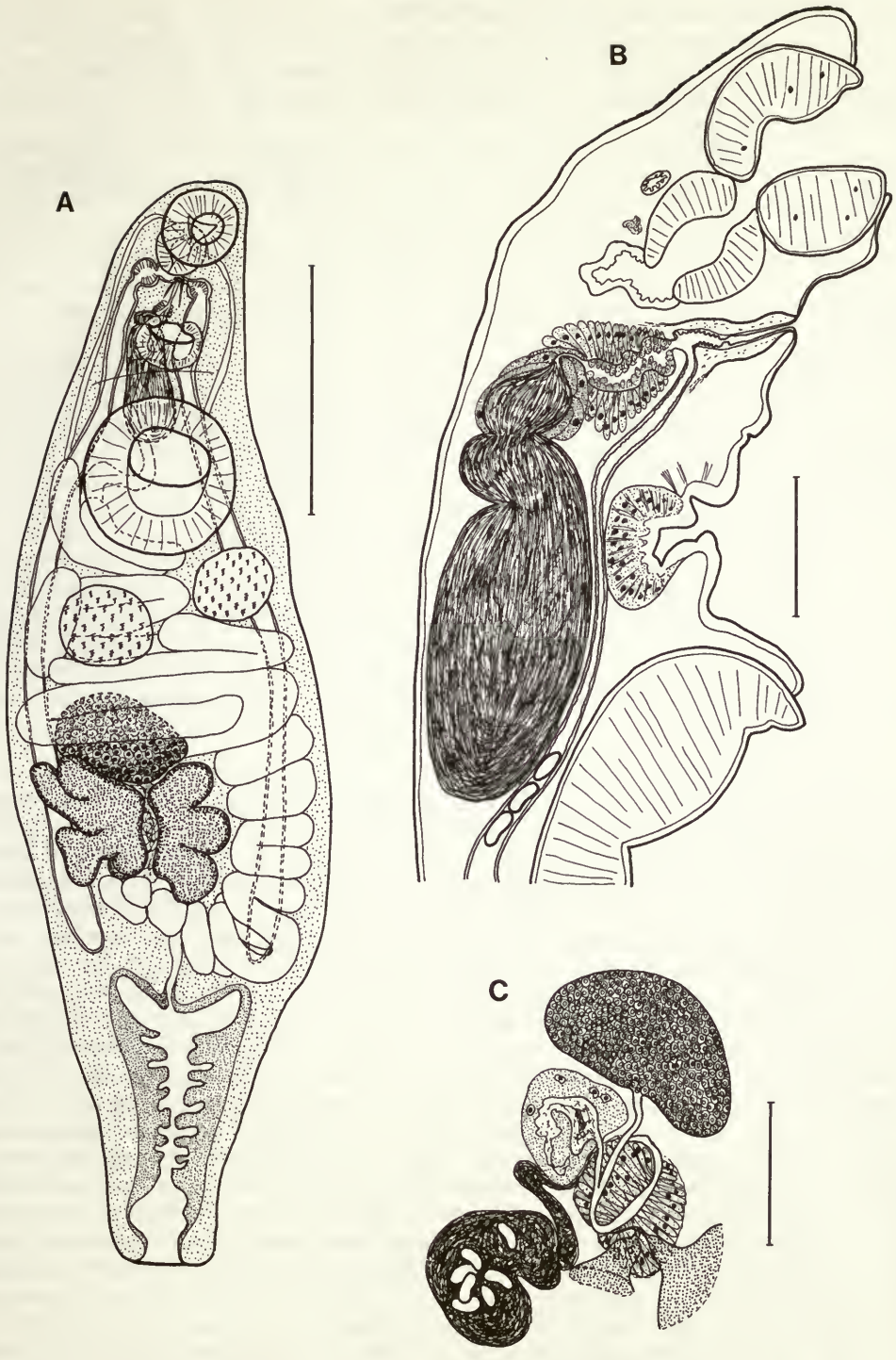

Fig. 27 *Synaptobothrium caudiporum* ex *Scophthalmus rhombus*. (A) Entire worm; (B) Sagittal section of forebody; (C) Lateral view of ovarian complex. Scale bars: A 500 μm; B,C 100 μm.

Table 14 Measurements of *Synaptobothrium caudiporum*

Authority	Odhner (1906)	Looss (1908)	Nikolaeva (1966)	Present material
Name used	*Lecithochirium copulans*	*S. caudiporum*	*S. caudiporum*	*S. caudiporum*
Host	*Arnoglossus laterna*	*Psetta maxima*	*Arnoglossus laterna* etc.	*Scophthalmus rhombus* etc.
Locality	Belgian coast	Trieste, Italy	Mediterranean Sea	NE Atlantic
Length (mm)	1·9–2·6	1·0–2·7	0·94–2·7	0·8–3·05
Breadth (mm)	0·65–1·0	up to 0·7	0·3–1·12	0·33–0·72
Ecsoma (mm)	–	–	–	0–0·45
Forebody (mm)	–	–	–	0·2–0·65
Oral sucker (mm)	0·13–0·24 diam.	0·13–0·2 diam.	0·07–0·21 × 0·1–0·22	0·1–0·21 × 0·12–0·21
Ventral sucker (mm)	0·25–0·4 diam.	0·25–0·4 diam.	0·13–0·39 × 0·16–0·46	0·2–0·47 × 0·21–0·46
Sucker-ratio	(1 : 1·65–1·9)*	1 : 2	(1 : 1·5–2·1)*	1 : 1·75–2·4
Testes (mm)	–	–	0·03–0·12 × 0·03–0·18	0·1–0·21 × 0·1–0·26
Ovary (mm)	–	–	0·1–0·31 × 0·11–0·39	0·11–0·28 × 0·13–0·36
Eggs (μm)	27–30 × 11	32 × 13	25–32 × 10–15	25–28 × 11–14 (ex *Zeus* 28–31 × 10–12)

*Ratios calculated from measurements in the literature.

The excretory pore is situated terminally on the ecsoma, i.e. at the anterior end of the ecsomal cavity in most of our material (Fig. 27A). It leads into a Y-shaped *excretory vesicle,* the tubular stem of which passes forward medially prior to bifurcating at a level just posterior to the ventral sucker. The two arms pass dorso-laterally into the forebody and unite dorsally to the pharynx.

The two oval to globular *testes* occur symmetrically or slightly obliquely in the ventro-lateral field a short distance posterior to the ventral sucker. Although separated, there are no uterine coils between them. The union of the vasa efferentia could not be seen in our material. The seminal vesicle is a bipartite, elongate-oval structure, which usually extends posteriorly to a level dorsal to the anterior half of the ventral sucker. The posterior part of this organ is large, saccular and normally appears to be constricted into two parts by a bend which occurs well within the anterior half (Fig. 27B). The distal, smaller part of the seminal vesicle has a slightly more muscular wall than the proximal part and is surrounded by a small number of large, granular cells, especially distally. It is tear-shaped, tapering to form a narrow duct which leads into the pars prostatica. The latter organ is tubular, but wide, and compared with the lecithochiriines, quite long. It possesses a dense covering of external gland-cells and a lining of anuclear blebs which almost fill the lumen. The pars prostatica, which can be straight to sigmoid, passes forward antero-ventrally and unites with the metraterm via a small sphincter within the open base of the sinus-sac to form the hermaphroditic duct. The region of the male duct within the sphincter may be all that remains of the ejaculatory duct. The *sinus-sac* is claviform, weakly developed and appears to be of the 'open'-type, as there is no evidence of its contact with the male or female ducts (Fig. 27B). The hermaphroditic duct is tubular and possesses, especially proximally, a muscular wall. It opens via the genital pore, which is situated mid-ventrally at about the level of the oesophagus. There is no genital atrium.

The transversely oval to irregularly oval *ovary* is situated in about the middle of the body (soma), although its exact position varies with contraction and the state of the ecsoma. It occurs

ventro-laterally on either side of the body, and is normally separated from the testis on the same side of the body by a distinct region of uterine coils. The oviduct leaves the ovary posteriorly. It passes back over the surface of Mehlis' gland, which is situated immediately posteriorly to the ovary, and receives the duct from Juel's organ. The latter organ occurs immediately postero-dorsal to the ovary (Fig. 27C) and closely applied to the surface of Mehlis' gland. As the oviduct passes into Mehlis' gland it appears to receive the very narrow common vitelline duct, but the exact junction could not be discerned in our material. The initial part of the uterus is very narrow, but this passes back over the surface of Mehlis' gland and coils postero-dorsally to the latter organ. Here it becomes wider and contains spermatozoa, thus forming a uterine seminal receptacle. The uterine loops then pass posteriorly on the ovarian side of the body to about the level of the base of the withdrawn ecsoma. Here they pass to the other side of the body and return anteriorly. When the ecsoma is extruded the uterus may extend into it. At about the level of the ovary, the uterine coils usually extend across the body dorsally and sometimes ventrally to the ovary, and normally fill the region of the body between the ovary and the testis on the ovarian side of the body. The coils continue anteriorly dorsal to and sometimes between the testes. Dorsally or dorso-laterally to the ventral sucker they narrow and the undulations become smaller until, close to the proximal end of the seminal vesicle, the uterus becomes a narrow, muscular metraterm. This passes directly forward, ventral or ventro-lateral to the seminal vesicle, and unites with the male duct at the base of the sinus-sac. The uterus contains numerous narrow, slightly reniform eggs, which are quite long for a hemiurid. These eggs have thin walls and are very susceptible to collapse during the processing of whole-mounts. The *vitellarium,* which is situated immediately postero-ventral to the ovary, is composed of two symmetrical and juxtaposed masses. One of the masses generally has three lobes and the other four, the length of the lobes normally being from one to two times their width. The main vitelline ducts, which are initially short and broad, pass medially and appear to pass into Mehlis' gland. Distally they appear to be very narrow and unite to form a very narrow common duct, which presumably unites with the oviduct as it passes into Mehlis' gland.

Discussion. This species was originally recorded by Rudolphi (1819) from *Zeus faber* in the Adriatic Sea. A brief description of the type-material was given by Lühe (1901*b*); but the later more detailed descriptions of Odhner (1906) and Looss (1908) were based entirely or mainly on specimens from the flatfishes *Arnoglossus laterna* and *Psetta maxima.* Although Looss (1908) apparently possessed material from *Z. faber,* there is no detailed description based upon specimens from this host. After examining two specimens from *Z. faber,* including one removed from a fish in the Fish Collection of the BM(NH), we can confirm that they do appear to be conspecific with the material described from flatfishes, although it is worth noting that their eggs were slightly larger (Table 14), albeit within the range given by other authors.

In the Black Sea this parasite is claimed to occur in hosts such as *Sarda sarda* (see Butskaja, 1952; Pogorel'tseva, 1952) and *Trachurus mediterraneus ponticus* (see Nikolaeva, 1963; Kovaleva, 1970*a*); but aspects of their dimensions, i.e. egg-length, egg-breadth and sucker-ratio, indicate that these records require confirmation, especially as the morphologically similar *Lecithochirium musculus* occurs regularly in that region.

The use of egg-measurements for this species can be very misleading, as the eggs are thin-walled and very susceptible to collapse during dehydration. Our measurements of the length of collapsed eggs in whole-mounts were several micrometres less than those taken from sections or from specimens mounted in glycerine jelly. Great care is, therefore, required when using this criterion, not only in relation to one's own material, but also in the use of data taken from the literature.

Host-parasite list

Order Petromyzoniformes

Lampetra fluviatilis (Linnaeus): (?) *Hemiurus communis* Odhner

Order Acipenseriformes

Acipenser sturio Linnaeus: (?) *Hemiurus communis* Odhner

Order Rajiformes

Torpedo marmorata Risso: (?) *Hemiurus communis* Odhner

Order Clupeiformes

Alosa alosa (Linnaeus): *Hemiurus appendiculatus* (Rudolphi)
Alosa fallax (Lacepède): *Hemiurus appendiculatus* (Rudolphi)
Clupea harengus Linnaeus: *Brachyphallus crenatus* (Rudolphi)
Hemiurus luehei Odhner
Sardina pilchardus (Walbaum): *Hemiurus luehie* Odhner
Sprattus sprattus (Linnaeus): *Hemiurus luehei* Odhner

Order Anguilliformes

Anguilla anguilla (Linnaeus): *Hemiurus communis* Odhner
Lecithochirium furcolabiatum (Jones)
(?) *Lecithochirium musculus* (Looss)
Lecithochirium rufoviride (Rudolphi)
Conger conger (Artedi, in Linnaeus): *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Lecithochirium furcolabiatum (Jones)
Lecithochirium fusiforme Lühe
(?) *Lecithochirium musculus* (Looss)
Lecithochirium rufoviride (Rudolphi)
Synaptobothrium caudiporum (Rudolphi)

Order Salmoniformes

Argentina sphyraena (Linnaeus): *Hemiurus communis* Odhner
Coregonus lavaretus oxyrinchus (Linnaeus): *Hemiurus communis* Odhner
Osmerus eperlanus (Linnaeus): *Brachyphallus crenatus* (Rudolphi)
(?) *Lecithochirium rufoviride* (Rudolphi)
Salmo salar Linnaeus: *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Hemiurus levinseni Odhner
Hemiurus luehei Odhner
Salmo trutta Linnaeus: *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Hemiurus luehei Odhner
Lecithochirium musculus (Looss)
Xenodermichthys socialis Vaillant: *Dinosoma ventrovesicularis* sp. nov.

Order Gadiformes

Arctogadus sp. [?*pearyi* (Nichols & Maxwell)]: *Hemiurus levinseni* Odhner
Boreogadus saida (Lepechin): *Hemiurus levinseni* Odhner
Brosme brosme (Ascanius): *Hemiurus communis* Odhner
Ciliata mustela (Linnaeus): *Hemiurus communis* Odhner
Lecithochirium furcolabiatum (Jones)
Coryphaenoides rupestris Gunnerus: *Glomericirrus macrouri* (Gaevskaja)
Gadus morhua Linnaeus: *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Hemiurus levinseni Odhner
Hemiurus luehei Odhner
(?) *Lecithochirium rufoviride* (Rudolphi) [encapsulated]
Synaptobothrium caudiporum (Rudolphi)

Gaidropsarus mediterraneus (Linnaeus): *Hemiurus communis* Odhner
(?) *Lecithochirium furcolabiatum* (Jones) [encapsulated]
Gaidropsarus vulgaris (Cloquet): *Hemiurus communis* Odhner
(?) *Lecithochirium furcolabiatum* (Jones) [encapsulated]
Macrourus berglax Lacepède: (?) *Glomericirrus macrouri* (Gaevskaja)
Melanogrammus aeglefinus (Linnaeus): *Hemiurus communis* Odhner
Merlangius merlangus (Linnaeus): *Hemiurus communis* Odhner
Hemiurus levinseni Odhner
Hemiurus luehei Odhner
Merluccius merluccius (Linnaeus): *Hemiurus communis* Odhner
Hemiurus levinseni Odhner
Hemiurus luehei Odhner
Micromesistius poutassou (Risso): *Hemiurus communis* Odhner
Hemiurus levinseni Odhner
Molva molva (Linnaeus): *Hemiurus communis* Odhner
(?) *Lecithochirium fusiforme* Lühe [imm.]
(?) *Lecithochirium rufoviride* (Rudolphi) [imm.]
Nezumia aequalis (Günther): *Glomericirrus macrouri* (Gaevskaja)
Phycis blennoides (Brünnich): *Hemiurus communis* Odhner
Hemiurus levinseni Odhner
Pollachius pollachius (Linnaeus): *Hemiurus communis* Odhner
(?) *Hemiurus levinseni* Odhner
Hemiurus luehei Odhner
Pollachius virens (Linnaeus): *Hemiurus communis* Odhner
(?) *Hemiurus levinseni* Odhner
Raniceps raninus (Linnaeus): *Hemiurus communis* Odhner
Trachyrincus trachyrincus (Risso): *Glomericirrus macrouri* (Gaevskaja)
Trisopterus esmarkii (Nilsson): *Hemiurus communis* Odhner
Hemiurus levinseni Odhner
Trisopterus luscus (Linnaeus): *Hemiurus communis* Odhner
(?) *Hemiurus levinseni* Odhner
(?) *Lecithochirium musculus* (Looss)
Synaptobothrium caudiporum (Rudolphi)
Trisopterus minutus (Linnaeus): *Hemiurus communis* Odhner
Hemiurus levinseni Odhner

Order Beryciformes

Hoplostethus atlanticus Collet: *Hemiurus communis* Odhner
Glomericirrus macrouri (Gaevskaja)

Order Zeiformes

Capros aper (Linnaeus): *Hemiurus communis* Odhner
Hemiurus luehei Odhner
Zeus faber Linnaeus: *Synaptobothrium caudiporum* (Rudolphi)

Order Syngnathiformes

Entelurus aequoreus (Linnaeus): *Hemiurus communis* Odhner

Order Gasterosteiformes

Gasterosteus aculeatus Linneaus: *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Spinachia spinachia (Linnaeus): *Brachyphallus crenatus* (Rudolphi)

Order Scorpaeniformes

Aspitrigla cuculus (Linnaeus): *Hemiurus communis* Odhner
Cyclopterus lumpus Linnaeus: *Hemiurus communis* Odhner

Eutrigla gurnardus (Linnaeus): *Hemiurus communis* Odhner
Hemiurus levinseni Odhner
Hemiurus luehei Odhner
Liparis montagui (Donovan): *Hemiurus communis* Odhner
Myoxocephalus scorpius (Cuvier): *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Sebastes marinus (Linnaeus): *Hemiurus communis* Odhner
Taurulus bubalis (Euphrasen): *Hemiurus communis* Odhner
(?) *Lecithochirium furcolabiatum* (Jones) [encapsulated]
(?) *Synaptobothrium caudiporum* (Rudolphi) [encapsulated]
Trigla lucerna Linnaeus: *Hemiurus communis* Odhner
Synaptobothrium caudiporum (Rudolphi)
Trigloporus lastoviza (Brünnich): *Hemiurus communis* Odhner
Hemiurus luehei Odhner

Order Perciformes

Ammodytes marinus Raitt: *Hemiurus communis* Odhner
Ammodytes tobianus Linnaeus: (?) *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Blennius pholis Linnaeus: *Hemiurus communis* Odhner
Lecithochirium furcolabiatum (Jones) [encapsulated]
(?) *Lecithochirium rufoviride* (Rudolphi) [encapsulated]
(?) *Synaptobothrium caudiporum* (Rudolphi) [encapsulated]
Brama brama (Bonnaterre): *Hemiurus luehei* (Odhner)
Coryphoblennius galerita (Linnaeus): (?) *Lecithochirium furcolabiatum* (Rudolphi) [encapsulated]
Dicentrarchus labrax (Linnaeus): *Hemiurus communis* Odhner
Epigonus telescopus (Risso): *Hemiurus communis* Odhner
Gobius niger Linnaeus: *Hemiurus communis* Odhner
Gobius paganellus Linnaeus: *Hemiurus communis* Odhner
(?) *Lecithochirium furcolabiatum* (Jones) [encapsulated]
Gobiusculus flavescens (Fabricius): *Lecithochirium musculus* (Looss)
Hyperoplus lanceolatus (Le Sauvage): *Hemiurus communis* Odhner
Labrus bergylta Ascanius: *Hemiurus communis* Odhner
(?) *Lecithochirium furcolabiatum* (Jones) [encapsulated]
(?) *Synaptobothrium caudiporum* (Rudolphi) [encapsulated]
Leptoclinus maculatus (Fries): *Brachyphallus crenatus* (Rudolphi)
Pagellus bogareveo (Brünnich): *Hemiurus communis* Odhner
Pholis gunnelus (Linnaeus): *Hemiurus communis* Odhner
Pomatoschistus minutus (Pallas): *Synaptobothrium caudiporum* (Rudolphi)
Pomatoschistus pictus (Malm): *Lecithochirium musculus* (Looss)
Scomber japonicus Houttuyn: (?) *Lecithocladium excisum* (Rudolphi)
Scomber scombrus Linnaeus: *Hemiurus luehei* Odhner
Lecithocladium excisum (Rudolphi)
Symphodus melops (Linnaeus): (?) *Synaptobothrium caudiporum* (Rudolphi) [encapsulated]
(?) *Lecithochirium furcolabiatum* (Rudolphi) [encapsulated]
Trachinus draco Linnaeus: *Hemiurus communis* Odhner
Trachurus trachurus (Linnaeus): *Hemiurus communis* Odhner
Hemiurus luehei Odhner
Ectenurus lepidus Looss
Lecithocladium excisum (Rudolphi)
Zoarces viviparus (Linnaeus): *Hemiurus communis* Odhner
(?) *Lecithochirium rufoviride* (Rudolphi)

Order Gobiesociformes

Lepadogaster lepadogaster (Bonnaterre): *Hemiurus communis* Odhner

Order Pleuronectiformes

Arnoglossus laterna (Walbaum): *Synaptobothrium caudiporum* (Rudolphi)
Hippoglossoides platessoides (Fabricius): *Hemiurus communis* Odhner
Hippoglossus hippoglossus (Linnaeus): *Hemiurus communis* Odhner
Hemiurus levinseni Odhner
Limanda limanda (Linnaeus): *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Platichthys flesus (Linnaeus): *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Hemiurus luehei Odhner
Lecithochirium musculus (Looss)
Pleuronectes platessa Linnaeus: *Brachyphallus crenatus* (Rudolphi)
Hemiurus communis Odhner
Synaptobothrium caudiporum (Rudolphi)
Psetta maxima (Linnaeus): (?) *Lecithochirium rufoviride* (Rudolphi) [encapsulated]
Reinhardtius hippoglossoides (Walbaum): *Brachyphallus crenatus* (Rudolphi)
Scophthalmus rhombus (Linnaeus): *Hemiurus communis* Odhner
(?) *Lecithochirium rufoviride* (Rudolphi)
Synaptobothrium caudiporum (Rudolphi)
Solea solea (Linnaeus): *Hemiurus communis* Odhner
Zeugopterus punctatus (Bloch): *Hemiurus communis* Odhner

Order Lophiiformes

Lophius piscatorius Linnaeus: *Hemiurus communis* Odhner
Lecithochirium fusiforme Lühe [imm.]
Lecithochirium rufoviride (Rudolphi)
Synaptobothrium caudiporum (Rudolphi)

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Rodney A. Bray & David I. Gibson

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Synopsis

Keys, original descriptions, lists of synonyms, full host-records, locality data and comments on some aspects of their biology are presented for all of the zoogonid species recorded from the north-eastern Atlantic region. The species described are *Zoogonus rubellus, Diphterostomum brusinae, D. betencourti, D. vividum* n. comb., *Pseudozoogonoides subaequiporus* n. comb., *Pseudozoogonoides* sp. innom., *Zoogonoides viviparus, Lepidophyllum steenstrupi, L. appyi* sp. nov., *Panopula bridgeri* sp. nov., *P. spinosa* n. comb., *Brachyenteron pycnorganum, B. campbelli* sp. nov., *Steganodermatoides maceri* sp. nov., *Neosteganoderma glandulosum, Proctophantastes abyssorum* and *Steganoderma (Lecithostaphylus) retroflexum.*

In addition, *Zoogonus lasius* from the north-west Atlantic is considered distinct from *Z. rubellus*. The new combination *Proctophantastes gillissi* is formed.

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Introduction

This is the fifth in a series of papers in which the digenean fauna of the marine fishes of the north-eastern Atlantic is discussed (see Bray & Gibson, 1977, 1980; Gibson & Bray, 1977, 1986). The family treated is the Zoogonidae, a widespread group, restricted to fishes, mainly marine but with a few freshwater examples. One of us has completed a general taxonomic review of the family Zoogonidae (Bray, 1985*b*, in press *a*,*b*).

Materials and methods

The materials used in this investigation and the areas of study are as outlined by Bray & Gibson (1977). The collecting trips undertaken are as reported in previous contributions in this series, but also include the northern North Sea and off northern Scotland aboard DAFS RV *Scotia* in 1985 (by R.A.B). The taxonomic methods used are outlined in the general review articles (Bray, 1985*b*, in press *a*,*b*).

Systematic section

Family **ZOOGONIDAE** Odhner, 1902

Steganodermatidae Yamaguti, 1934.

Diagnostic features. Body small to large, elongate cylindrical to flattened spatulate. Body surface usually spinose. Ventral sucker small to large; simple, ornamented or transversely divided. Prepharynx long to absent. Oesophagus long to absent, bifurcates in forebody to anterior hindbody. Caeca two, short saccular to long; terminating in forebody to reaching to posterior extremity. Cirrus-sac well developed. Genital pore marginal or submarginal, usually sinistral. Ovary usually pre-testicular. Seminal vesicle and Laurer's canal present. Uterus usually reaches to posterior extremity. Eggs with tanned shells or membranous capsules. Vitellarium single or double mass or follicular. Excretory pore terminal, vesicle short saccular to long tubular I-shaped. In alimentary canal, gall-bladder, bile-duct of urinary bladder or teleosts or occasionally elasmobranchs.

Key to the subfamilies

1 Vitellarium median, small globular or bilobed mass. Egg capsules membranous or very weakly tanned . . . . . **ZOOGONINAE** Odhner, 1902 (p. 128)
– Vitellarium follicular in two lateral symmetrical fields. Egg capsules strongly tanned, forming shells . . . . . **LEPIDOPHYLLINAE** Stossich, 1903 (p. 160)

Subfamily **ZOOGONINAE** Odhner, 1902

Key to the genera of the Zoogoninae from the north-east Atlantic

1 Vitelline mass single. 2
— Vitelline mass bilobed (double). 3
2 Genital pore and intestinal bifurcation in mid-forebody. Caeca narrow . . . . . *Zoogonoides* Odhner, 1902 (p. 151)
— Genital pore at level of ventral sucker. Intestinal bifurcation dorsal to ventral sucker or in hindbody. Caeca short, saccular . . . . . *Zoogonus* Looss, 1901, (p. 129)
3 Caeca short, saccular, divergent. No atrial sac. Muscular lamellar lips may occur on ventral sucker. Ovary pre- or inter-testicular . . . . *Diphterostomum* Stossich, 1903 (p. 135)
— Caeca long, parallel. Atrial sac present. No muscular lips on ventral sucker . . . . . *Pseudozoogonoides* Zhukov, 1957 (p. 146)

Genus *ZOOGONUS* Looss, 1901

DIAGNOSTIC FEATURES. Prepharynx distinct, short to long. Oesophagus bifurcates dorsally to ventral sucker or in anterior hindbody. Caeca short saccular. Cirrus-sac elongate with bipartite seminal vesicle. Genital pore marginal at about level of ventral sucker. Ovary globular to oval, between caeca. Vitellarium single, globular. Egg-capsule membranous. Excretory vesicle short sac. Sporocysts in gastropods. Tail-less xiphidiocercaria. Metacercariae in echinoderms, polychaetes and gastropods. Adults in marine teleosts.

COMMENT. Only one species occurs in the north-east Atlantic.

Zoogonus rubellus (Olsson, 1868) Odhner, 1902

Distoma rubellum Olsson, 1868.
Lecithodendrium rubellum (Olsson, 1868) Stossich, 1899.
Zoogonus mirus Looss, 1901.
(?) *Cercariaeum reticulatum* Stunkard, 1932.
(?) *Zoogonus* sp. of Richard (1971).

TYPE-HOST AND LOCALITY. *Labrus bergylta,* Bergen, Norway.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Anarhichas lupus [posterior intestine] Kristineberg, Sweden (Jan. 1971). Material studied for us by J. Thulin.
—— [rectum] Off NE Scotland (58°N, 00°; depth 99–111 m; & 59°N, 01°E; depth 107–117 m; Dec. 1979) BM(NH) 1982.1.20.1–5; Bell Rock, North Sea (56°N, 02°E; depth 52 m; May 1982) and Copinsay, North Sea (59°N, 02°W; depth 75 m; June 1983) BM(NH) 1983.11.23.19–22.
Labrus bergylta [intestine] Kristineberg, Sweden (Aug. 1976). BM(NH) 1982.1.20.6–7.
Labrus bimaculatus [intestine] Plymouth, Devon, England (May 1932). BM(NH) 1932.11.25.53–64 (see Baylis & Jones, 1933: 630).
Limanda limanda [intestine] Plymouth, Devon, England (May, 1932). BM(NH) 1932.11.25.65–66 (see Baylis & Jones, 1933: 630
Platichthys flesus [rectum] Plymouth, Devon, England (May 1972). BM(NH) 1982.1.20.8
Pleuronectes platessa [intestine, rectum] Plymouth, Devon, England (May 1972). BM(NH) 1982.1.20.9–10.

(b) From elsewhere
None

(ii) NE Atlantic records from the literature
Anarhichas lupus [rectum, lower intestine] St Andrews Bay, Scotland. Nicoll (1909*a*: 17).
Blennius pholis [rectum] Roscoff, Finistère, France. Sproston (1939: 40).
Labrus bergylta [intestine] Bergen, Norway. Olsson (1868: 40).
—— [?] Kristineberg, Sweden. Odhner (1902: 59).
Labrus bimaculatus [intestine] Plymouth, Devon, England. Baylis & Jones (1933: 630); Baylis (1939: 483).
Limanda limanda [intestine] Plymouth, Devon, England. Baylis & Jones (1933: 630); Baylis (1939: 483).
Pleuronectes platessa [?] Roscoff, Finistère, France. Sproston (1939: 40).
Trachurus trachurus [intestine] near Straits of Gibraltar. Kovaleva (1969: 132; 1970: 52); Gaevskaya & Kovaleva (1980*a*: 53; 1980*b*: 19; 1982: 61).

ASPECTS OF BIOLOGY
Records of larval stages in the NE Atlantic:

(a) First intermediate host
Nassarius reticulatus [?] St. Efflam, Côtes du Nord, Finistère, France. Richard (1971: 154; as *Zoogonus* sp.).
—— [digestive gland] Roscoff, Finistère, France. Stunkard (1932: 339; as *Cercariaeum reticulatum*).

(b) Second intermediate host
Psammechinus miliaris [muscles and connective tissue of Aristotle's lantern] Wimereux region, Artois, France. Stunkard (1941: 208).

Stunkard (1941) believed that there might be a biological distinction between *Z. rubellus* in the north-eastern Atlantic and Mediterranean Sea and the form *Z. lasius* in the north-western Atlantic. He not only emphasized apparent differences in life-cycle, but pointed out that, according to Goldschmidt (1905), *Z. rubellus (=mirus)* had 10 chromosomes and the North American form had 12 according to Brooks (1930). Benazzi & Benazzi Lentati (1976), however, stated that Goldschmidt's observations were disputed by Schreiner & Schreiner (1908), Grégoire (1909) and Wassermann (1913), all of whom say 2n=12 in *Z. mirus*. The differences that Stunkard (1941) detected in the life-cycle included the observation that, whereas at Wimereux in Northern France he found the metacercariae commonly in the sea-urchin *(Psammechinus miliaris)*, he failed to find the cercariae in over 1200 specimens of *Nassarius reticulatus* from the same region, although he found *Cercariaeum reticulatum* at Roscoff. Earlier (1933, 1936, 1938) Stunkard had completed the life-cycle of the North American form and had found that *Nassarius obsoletus* was the first intermediate host and the annelid *Nereis virens* the second intermediate host. In 1941 he failed to find *Zoogonus* metacercariae in nereids around Wimereux and in sea-urchins in Massachusetts. He was, however, able to experimentally infest the echinoid *Arbacia punctulatus* with the North American form. He considered the 'data on *Zoogonus* are hard to interpret. In view of the lack of specificity in life-cycles of their trematodes, it is not impossible that a single species of *Zoogonus* employs different primary, secondary and definitive hosts on the two sides of the Atlantic Ocean'. The metacercaria of the North American form has since (Stunkard, 1972) been found in the limpet *Acmaea intestinalis*, indicating that a wide range of invertebrates serve as second intermediate hosts for this species. A number of minor morphological differences between the larval stages of the North American and European forms are mentioned by Stunkard (1941), but these do not appear to be sufficient to distinguish these forms as species in the absence of other evidence. We have been able to examine adult specimens of the North American form *Z. lasius* from the posterior intestine of *Leiostomus xanthurus* (Sciaenidae) (BM(NH) 1983.11.1.1–8) and *Trinectes maculatus* (Soleidae) (BM(NH) 1983.11.1.9.) from Lower Chesapeake Bay, Virginia, USA (collector: E. M. Burreson) and from *Menidia menidia* (Atherinidae) (BM(NH) 1985.1.16.2–3) from Sam Orr Pond, near St Andrews, New Brunswick, Canada (collector: R.A.B). Their dimensions are included on Table 1. There seems to be a consistent difference between these forms and *Z. rubellus* from the north-east Atlantic, in that the suckers are relatively distinctly smaller and the prepharynx longer and usually narrower. These features are so striking when comparing specimens (Figs 1, 2) that it appears most prudent to consider *Z. lasius* distinct. It should also be noted that, despite a reasonable amount of collecting in the area, no *Zoogonus* specimens have been found in the Iceland/Greenland region which suggests that there is a discontinuity in the distribution of these forms. The work of Stunkard (1938, 1941) has shown that *Cercariaeum lintoni* Miller & Northup, 1926 is the larval form of the American species, *Z. lasius*, and that *C. reticulatum* is likely to be identical to the European species, *Z. rubellus*.

The first intermediate host of *Z. rubellus* is, therefore, most probably *Nassarius reticulatus*. *Cercariaeum reticulatum*, as described by Stunkard (1932), is a tail-less xiphidiocercaria emanating from the digestive gland of the host. In 1941 Stunkard believed it to be a larval *Zoogonus*, although originally he pointed out its similarity to the larva of *Diphterostomum brusinae*. It differs from the *D. brusinae* cercaria, however, in that it lacks a very large ventral sucker with muscular lips and possesses a long prepharynx. In fact *C. reticulatum* is very similar to the larva of *Z. lasius*, also known as *Cercariaeum lintoni*, which has been described by Leidy (1891), Linton (1915), Miller & Northup (1926), Africa (1930), Shaw (1933) and Stunkard (1938).

The host-parasite relationships of the larval stages of *Z. lasius* (often as *Z. rubellus*) are surprisingly well studied considering the rather small amount of work done on the adult form. A number of studies have been undertaken on the eastern coast of the USA which may be relevant to the biology of *Z. rubellus* in the north-eastern Atlantic. These studies have usually involved the first intermediate host, *Nassarius obsoletus*, a snail which is also regularly infested with a number of other digeneans. The sporocyst generations were described by Stunkard (1938) – rediae do not occur. The seasonal prevalence in *N. obsoletus* was studied on Rhode Island by Gambino (1959) and in North Carolina by McDaniel & Coggins (1971, 1972). Gambino found that May saw the peak of infestation, and also found that the higher rate of infestation was to be found in the

Table 1 Measurements of *Zoogonus lasius*

Authority	Stunkard (1938)	Present study		
Name used	*Zoogonus rubellus*	*Zoogonus lasius*		
Host	4 fish spp. (3 expl)	*Leiostomus xanthurus*	*Trinectes maculatus*	*Menidia menidia*
Locality	Massachusetts	Chesapeake Bay	Chesapeake Bay	New Brunswick
Length (mm)	0·7–1·2	0·94–1·05	0·84	0·76–1·2
Breadth (mm)	0·18–0·28	0·15–0·18	0·18	0·20–0·26
Length : forebody ratio	–	1 : 0·37–0·42	1 : 0·35	1 : 0·22–0·26
Oral sucker (mm)	0·07–0·08 diam.	0·04–0·06 × 0·05–0·06	0·08 × 0·07	0·07–0·08 × 0·08
Ventral sucker (mm)	0·075–0·085 diam.	0·06–0·08 × 0·07–0·08	0·09 × 0·08	0·09–0·10 × 0·09–0·12
Sucker-ratio	–	1 : 1·3–1·4	1 : 1·1	1 : 1·1–1·5
Prepharynx (mm)	–	0·25–0·31	0·17	0·11–0·12
Pharynx (mm)	0·04–0·06 diam.	0·03–0·05 × 0·04–0·05	0·06 diam.	0·06 × 0·04–0·05
Oesophagus (mm)	–	0·17–0·24	0·17	?
Cirrus-sac (mm)	–	0·15–0·20 × 0·04–0·05	0·17 × 0·04	0·16 × 0·05
Testes (mm)	0·032–0·073 diam.	0·12–0·13 × 0·09	0·08 × 0·05–0·06	0·10–0·11 × 0·07–0·08
Ovary (mm)	0·04–0·06	0·08 diam.	0·07 × 0·06	?
Miracidium (μm)	90–120 × 36–45 (fixed) 100–130 × 45–56 (alive)	94–128 × 40–47	102–137 × 50–59	110–120 × 45

high-tide zone. Sindermann (1960) reported that *Z. lasius* (as *Z. rubellus*), along with other larval digeneans, retarded or inhibited the offshore migration of the snail host, thus contributing to the relatively high inshore prevalence in autumn, and leaving the snails in a progressively more unfavourable environment, the high-tide zone, in winter. Laboratory experiments on the locomotion of infested and uninfested *N. obsoletus* by Stambaugh & McDermott (1969) supplemented Sindermann's findings. Schaefer, Milch & Levin (1970) found that a *Zoogonus* infection 'decreases the ability of the snail host to withstand dessication'. This may have a serious effect on the parasitized snails which are 'reluctant' to undergo their seasonal migration offshore. Further effects of *Z. lasius* infestation on *N. obsoletus* were investigated by Vernberg & Vernberg (1963, 1967) who found that the snail's resistance to thermal stress was reduced, and later (1971) they showed that *Z. lasius* metacercariae had a similar effect on their annelid host, *Leonereis culverti.* Riel (1975), on the other hand, found that infected *N. obsoletus* survived higher temperatures than uninfested and explained the discrepancy with earlier findings by suggesting seasonal differences. He also found that infested snails survived longest in distilled water. The cytochrome-c-oxydase activity and fatty acid composition of *N. obsoletus* digestive gland tissue were found by Vernberg (1969) and Lunetta & Vernberg (1971), respectively, to be altered by *Z. lasius* infestation, and it was suggested that this effect played a role in the lowered resistance to thermal stress reported at that time. Protein content in infested snail digestive gland decreased sharply (by 50 %) according to Schilansky, Levin & Fried (1977). A further result of *Z. lasius* infestation of *N. obsoletus*

is, according to Cheng, Sullivan & Harris (1973), 'direct chemical castration' and this prompted these authors to suggest that *Z. lasius* could represent a possible biological control agent of *Austrobilharzia variglandis* (Miller & Northup, 1926), the cause of 'swimmer's itch', the larvae of which also parasitize *N. obsoletus*.

Studies of the various larval digeneans found in *N. obsoletus* have shown that the thermal toleration of various larval parasites and the host are unconnected (Vernberg & Vernberg, 1965, 1966, 1968), and, therefore, 'each species of parasite retains its own physiological integrity' (Vernberg & Vernberg, 1965). 'The response of the larvae sharing the same thermal environment differs so greatly that one can conclude that this is a genetically predetermined response which is not markedly influenced by the thermal environment of the intermediate host' (Vernberg & Vernberg, 1966). Vernberg (1961*a*,*b*) contrasted the temperature tolerance of the cercariae of *Himasthla quissetensis* (Miller & Northup, 1926), which has gulls as its final host, and *Z. lasius*, and found that while *Z. lasius* cercariae cannot survive temperatures above 39 °C, *H. quissetensis* cercariae can tolerate 41 °C for prolonged periods. Vernberg correlated these findings with the body temperature of the definitive hosts of these species and suggested (1968) that this 'could well reflect a physiological preadaptation'.

Z. lasius was found to be more frequently involved in double infections than any of the other six relatively common digenean parasites of *N. obsoletus*. Vernberg, Vernberg & Beckerdite (1974) found that 12 out of 14 double infestations involved *Z. lasius*, and De Coursey & Vernberg (1974) found that 57 % of the double infestations of *Z. lasius* were with *Lepocreadium setiferoides* (Miller & Northup, 1926). Both species tend to shed cercariae in daylight, and *L. setiferoides* tends to suppress the shedding of *Z. lasius*. McDaniel & Coggins (1971, 1972), on the other hand, could not find more than one species shed by any individual snail. Although primarily found in the digestive gland, *Z. lasius* was found by De Coursey & Vernberg (1974) to spread to the gonadal area and the hepatopancreas in heavy infestations.

In Europe the metacercaria of *Z. rubellus* occurs in the connective tissue and muscles of Aristotle's lantern of sea-urchins. Timon-David (1933, 1934, 1937*a*, 1938) records it in *Paracentrotus lividus*, *Sphaerechinus granularis* and *Arbacia aequituberculata* in the Mediterranean, and experimental infestations (Timon-David, 1937*a*, 1938) of *Blennius gattorugine* yielded immature worms after 45 days. Stunkard (1941) described the metacercaria from the sea-urchin *Psammechinus miliaris* in northern Brittany. The metacercariae of *Z. lasius* in the USA are reported from the polychaetes *Nereis virens* (by Stunkard, 1938) and *Leonereis culverti* (by Vernberg & Vernberg, 1971) and the limpet *Acmaea intestinalis* (by Stunkard, 1972).

The distribution of *Z. rubellus* includes, in addition to the north-eastern Atlantic and the Mediterranean Sea, the Red Sea and the west coast of Africa. A wide range of teleosts have been recorded as definitive hosts; apparently Perciformes and Pleuronectiformes are the major groups implicated, but records from Clupeiformes and Zeiformes have been made. The records from *Trachurus trachurus* need confirmation as this fish does not prey on the known intermediate hosts of *Z. rubellus*.

PREVIOUS DESCRIPTIONS. Olsson (1868: 40; as *D. rubellum*); Looss (1901: 439; as *Z. mirus*); Goldschmidt (1902: 870; 1905: 607; as *Z. mirus*); Odhner (1902: 59; 1911*a*: 245); Nicoll (1909*a*: 17).

DESCRIPTION (Figs 1, 2A,B). Twenty-nine whole-mounts and ten sets of serial sections were examined. The largest, most highly developed worms are from *Anarhichas lupus* (Figs 1A, 2A,B). Measurements of this species are included in Table 2. The worms are very small and bear annular rows of very small tegumental spines. These reach posteriorly only as far as about the middle of the hindbody, and may not always be apparent at all. The subterminal *oral sucker* is more or less globular and leads to a distinct wide prepharynx and to an oval *pharynx* situated in about the mid-forebody. This gives rise to a long, wide oesophagus which is lined with tegument. It divides level with the posterior part of the ventral sucker or a little more posteriorly. There is a short, narrow region lined with tegument which leads to the wide, short, saccular caeca which are lined with epithelium. These caeca do not reach far into the posterior half of the hindbody, but as the hindbody apparently develops allometrically, this relationship varies with age. The *ventral sucker*,

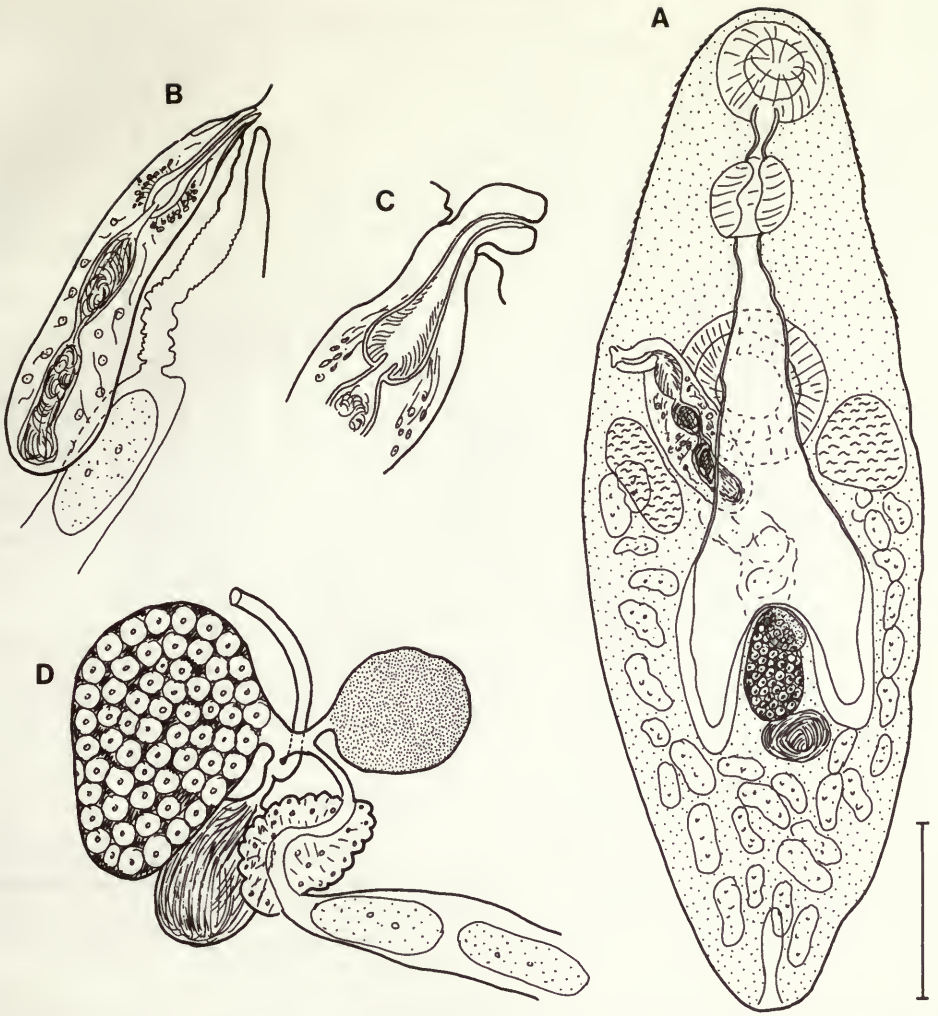


Fig. 1 *Zoogonus rubellus* (Olsson). (A) Dorsal view, ex *Anarhichas lupus*; (B) Terminal genitalia; (C) Everted cirrus; (D) Proximal female genitalia. Scale bar: A 0·2 mm.

which lies within the anterior half of the body, is similar in size to the oral sucker or may be slightly larger or smaller.

The *excretory pore* is terminal and leads into a short sac-like vesicle, which does not normally reach as far forward as the gonads.

The large oval *testes* lie symmetrically just posterior to the ventral sucker. It was not possible to fully trace the vasa efferentia, but there is, apparently, a very short vas deferens which divides close to the *cirrus-sac*. This latter organ is elongate and reaches well into the hindbody to about the level of the posterior margin of the testes and is often twisted distally. It contains a bipartite seminal vesicle which may be narrow (Fig. 1B) or bulbous (Fig. 2A), a short, vesicular pars prostatica and a narrow ejaculatory duct which is, apparently, not lined with spines. The remainder of the cirrus-sac is filled with gland-cells and connective tissue. A small genital atrium receives the ejaculatory duct beside the metraterm. The genital pore lies almost marginally at about the level of the middle of the ventral sucker and on the left side of the body. The cirrus is often everted a short way through the genital atrium (Fig. 1C).

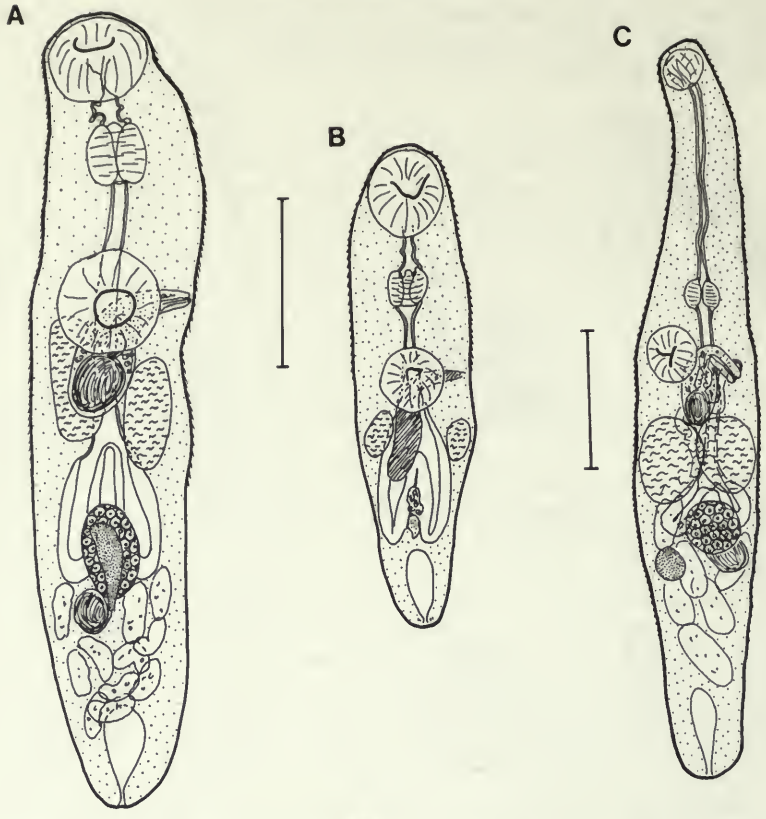


Fig. 2 *Zoogonus rubellus* (Olsson). (A) Ventral view, ex *Labrus bergylta*; (B) Ventral view of immature worm from *Pleuronectes platessa*; (C) *Zoogonus lasius* (Leidy), subventral view, ex *Leiostomus xanthurus*. Scale bars: A, B, C 0·2 mm.

The ovary, canalicular seminal receptacle and single, subglobular vitellarium are situated close together in the area between the short caeca. Unfortunately the ten sets of sectioned specimens do not clearly show the ducts which connect these organs, or Laurer's canal, although it appears that this latter organ opens on the dorsal surface at about the level of the ovary (Fig. 1D). The *ovary* lies more or less in the median line close to the dorsal surface with the seminal receptacle ventro-dextral and the vitellarium sinistral. The *vitellarium* is in the form of a small, subspherical body. The *uterus* fills the hindbody posterior to the gonads and passes forward to form a short, narrow, muscular metraterm apparently lined with fine spines. The uterus contains miracidia apparently surrounded by an egg-capsule, which may vary in thickness but is never tanned, being membranous. The eggs may be elongate in the uterus or packed closely and flattened at the ends. Thus measurements of eggs *in utero* are of limited taxonomic value.

Discussion. The validity of *Z. rubellus* and *Z. lasius* was discussed on p. 130. *Z. mirus*, the original type of the genus was considered a synonym of *Z. rubellus* by Nicoll (1909) and no one has seriously questioned this conclusion. Stunkard (1941) believed that 'at present there is no basis for a positive distinction between species of *Zoögonus* from the North Sea [i.e. *rubellus*] and the Mediterranean [i.e. *mirus*] ... ' We agree with this, there being no morphological or other features which have been raised to substantiate the validity of *Z. mirus*.

Table 2 Measurements of *Zoogonus rubellus* from various fishes

Host	*Anarhichas lupus*	*Labrus* spp.	Flatfish	Mean
Length (mm)	0·87–1·16	0·62–0·93	0·50–1·2	0·80
Breadth (mm)	0·35–0·40	0·19–0·32	0·15–0·56	0·29
Length : forebody ratio	1 : 0·30–0·345	1 : 0·30–0·35	1 : 0·34–0·48	1 : 0·35
Oral sucker (mm)	0·12–0·14 × 0·12–0·14	0·08–0·10 × 0·10–0·12	0·09–0·14 × 0·09–0·18	0·11 × 0·12
Ventral sucker (mm)	0·15–0·18 × 0·15–0·19	0·10–0·12 × 0·09–0·13	0·075–0·20 × 0·075–0·22	0·13 × 0·13
Sucker-ratio	1 : 1·24–1·36	1 : 0·9–1·2	1 : 0·9–1·4	1 : 1·12
Prepharynx (mm)	0·04–0·05	0·05	0·045–0·11	0·06
Pharynx (mm)	0·10 × 0·10	0·07 × 0·08	0·05–0·10 × 0·045–0·14	0·076 × 0·086
Oesophagus (mm)	0·22–0·37	–	0·06–0·22	0·20
Cirrus-sac (mm)	0·20–0·24 × 0·07–0·09	–	0·26–0·32 × 0·08–0·10	0·26 × 0·08
Testes (mm)	0·13–0·15 × 0·10	0·10–0·11 × 0·10–0·12	0·07–0·12 × 0·045–0·11	0·11 × 0·09
Ovary (mm)	0·13–0·17 × 0·08–0·12	–	–	0·15 × 0·09
Miracidium (μm)	85–135 × 47–55	immature	immature	

Genus ***DIPHTEROSTOMUM*** Stossich, 1903

Diphtherostomum Stafford, 1905.
Zoonogenus Nicoll, 1912.

DIAGNOSTIC FEATURES. Ventral sucker in middle or posterior of body, often large, muscular, sometimes smaller, more weakly developed; may bear muscular lips. Prepharynx short. Oesophagus normally distinct; caeca very short to short; terminating in posterior forebody to anterior hindbody. Testes oblique to symmetrical, in region of ventral sucker. Cirrus-sac variable. Seminal vesicle bipartite. Pars prostatica vesicular. Genital atrium distinct. Genital pore marginal to submarginal, in forebody; usually sinistral. Ovary subglobular, close to testes. Vitellarium consists of two subequal masses. Miracidium surrounded by membranous capsule or very thin shell. Excretory pore terminal, vesicle small, saccular. Sporocysts in gastropods. Tail-less xiphidiocercaria. Metacercariae encyst in invertebrates, occasionally on plants and sedentary animals. Adults in marine teleosts and elasmobranchs.

Key to *Diphterostomum* spp. found in the north-east Atlantic

1 Ventral sucker with muscular lips . . . . . *D. brusinae* (Stossich, 1888) (p. 135)
— Ventral sucker lacking muscular lips 2
2 Sucker ratio 1 : > 2·3; parasite of teleosts . . . . . *D. vividum* (Nicoll, 1912) (p. 144)
— Sucker ratio 1 : < 2·3; parasite of elasmobranchs . . *D. betencourti* (Monticelli, 1893) (p. 142)

Diphterostomum brusinae (Stossich, 1888) Stossich, 1903

Distoma brusinae Stossich, 1888.
Pleurogenes brusinae (Stossich, 1888) Stossich, 1899.
Distoma (Brachycaecum) brusinae (Stossich, 1888) Barbagallo & Drago, 1903.
(?) *Sporocystis* sp. de Filippi, 1854.

(?) *Distomum buccini mutabilis* de Filippi, 1855.
(?) *Cercaria (Acanthocephala) buccini mutabilis* (de Filippi, 1855) Diesing, 1858.
(?) *Agamodistomum buccini mutabilis* (de Filippi, 1855) Parona, 1912.
Cercaria inconstans Sinitsin, 1911.
Adolescaria inconstans Sinitsin, 1911.
(?) *Cercaria crispata* Pelseneer, 1906.
Diphterostomum sargus annularis Vlasenko, 1931.
Diphterostomum spari Yamaguti, 1938.
Diphterostomum macrosaccum Montgomery, 1957.
Diphterostomum anisotremi Nahhas & Cable, 1964.
Diphterostomum tropicum Durio & Manter, 1963.
Diphterostomum israelense Fischthal, 1980.

TYPE-HOST AND LOCALITY. *Oblada melanura*, Trieste, Italy.

RECORDS

(i) Material studied
(a) From the NE Atlantic
None.

(b) From elsewhere
Diplodus annularis [rectum, small intestine] Split, Yugoslavia (May, 1968), material lent by O. Sey (see Sey, 1970); and (Sept. 1975). BM(NH) 1982.4.21.1–2.
Lethrinus sp. [?] New Caledonia. Holotype of *D. tropicum*. USNM 63308.
Sillago analis [rectum] Deception Bay, Queensland, Australia. (Jan. 1981). Collector: G. Berry. BM(NH) 1982.12.22.38.
Sillago maculata [rectum] Deception Bay, Queensland, Australia. (Sept. 1980, 1981). Collector: G. Berry. BM(NH) 1982.12.22.14–37.
Symphodus tinca [rectum] Split, Yugoslavia. (Sept. 1975). BM(NH) 1982.4.21.3–12.

(ii) NE Atlantic records from the literature
Blennius ocellaris [intestine] Roscoff, Finistère, France. Sproston (1939: 40).
(?) *Diplodus vulgaris* [?] Oveido, Spain. Martinez Fernandez, in Cordero del Campillo (1975: 81; as *D.* sp., not described).

ASPECTS OF BIOLOGY

Records of larval stages in the NE Atlantic:

(a) First intermediate host
(?) *Natica alderi* [?] Boulogne, France. Pelseneer (1906: 171; as *Cercaria crispata*).
(?) *Nassarius reticulatus* [?] St Efflam, Finistère, France. Richard (1971: 151; as *D.* sp.).

(b) Second intermediate host
None.

Richard (1971) described the chaetotaxy of the cercaria she considered *Diphterostomum* sp. and Bayssade-Dufour & Maillard (1974), also using chaetotaxy, compared it with the cercariae of *D. brusinae* from *Nassa mutabilis* in the Mediterranean Sea. They concluded that Richard's cercaria belonged to the same genus, but did not comment as to whether they might be conspecific. Palombi (1930) also found the daughter-sporocyst in *Nassa mutabilis* in the Mediterranean. He found the sporocysts to contain about 20 cercariae in various stages of development. The cercaria itself is a tail-less xiphidiocercaria, without eyespots, and bears a prominant ventral sucker with the characteristic muscular lips. In *N. mutabilis* the metacercariae develop within the daughter-sporocysts and, therefore, this snail serves as both first and second intermediate hosts. On being fed to *Blennius gattorugine, Crenilabrus pavo* and *Sargus vulgaris* by Palombi, metacercariae developed to ovigerous adults in 40 days, the entire life-cycle requiring about six months. Other reports of the life-cycle (Dolgikh, 1965*a,b*, 1966*a,b*, 1968, 1970; Prévot, 1966; Zaika, 1966; Dolgikh & Naidenova, 1967; Gaevskaja, 1972; Zdun & Ignatyev, 1980*a,b*) suggest that it is rather variable and that a number of different types of organisms can be utilized as second intermediate host. Prévot

(1966) described a metacercaria from the crinoid *Antedon mediterranea*, and Zaika (1966) described a metacercaria similar to *D. brusinae* in the cephalochordate *Branchiostoma lanceolatus*. Dolgikh & Naidenova (1967) and other workers in the Black Sea region discovered the cercaria *('Cercaria inconstans')* from *Nassa reticulata* and *Cyclonassa kamyschiensis*. In addition to encysting within the daughter sporocyst in the gastropod and passing to lamellibranch second intermediate hosts *(Venus, Pitar, Gouldia, Spisula, Modiolus, Chamelea, Parvicardium)* to encyst, the cercariae may also encyst on plants, sponges and hydroids. This flexibility and variability of the life-cycle is reflected in considerable morphological variability in the adult.

The adult is normally to be found in the posterior intestine and rectum of perciform teleosts, notably of the families Sparidae, Gobiidae, Labridae, Pomadasyidae and Blenniidae. Most records are from the Mediterranean and Black Seas, with occasional reports from the north Atlantic, Caribbean Sea and Gulf of Mexico, Arabian Sea and North Pacific Ocean, Queensland (Australia), New Zealand, New Caledonia and south-west Atlantic.

PREVIOUS DESCRIPTIONS. Stossich (1888: 99; 1889: 25); Looss (1901: 399); Palombi (1930: 111); Vlasenko (1931: 103; as *D. sargus annularis*); Yamaguti (1934: 400; 1938: 92; as *D. spari*); Timon-David (1937*b*: 3); Montgomery (1957: 16; as *D. macrosaccum*); Ergens (1960: 80; as *D. spari*); Nahhas & Cable (1964: 200; as *D. anisotremi*); Brinkmann (1967: 6); Naidenova (1967: 488); Durio & Manter (1968: 152; as *D. tropicum*); Fischthal & Thomas (1968: 139; As *D. anisotremi*); Fischthal (1980: 14; as *D. israelense*); Amato (1983: 692; as *D. anisotremi*).

DESCRIPTION (Figs 3a–c, 4, 5). Five whole-mounts from *Diplodus annularus* and 11 whole-mounts and two sets of serial sections from *Symphodus tinca* were studied along with eight whole-mounts from *Sillago maculata*, three whole-mounts from *Sillago analis* and the holotype of *D. tropicum*. While much of the morphology of these worms from all hosts is similar, striking differences in the structure of the cirrus-sac will be described below. The measurements of this worm are given in Table 3. The worms are elongate oval (Figs 4A, 5), bearing annular rows of acuminate tegumental spines (Fig. 3A) reaching posteriorly to the region of the ventral sucker. The subterminal to terminal (Fig. 5) *oral sucker* leads, via a short prepharynx, into a small, globular *pharynx*. This, in turn, leads to a distinct, long, oesophagus which bifurcates in the posterior forebody. The caeca are short, and somewhat saccular, overlapping the ventral sucker slightly or to about its middle. The large *ventral sucker* lies mainly in the posterior half of the body. It is strongly muscular and has protruding lamellar muscular anterior and posterior lips (Fig. 3b,c).

The *excretory pore* is terminal and leads via a short, narrow duct into a small, globular vesicle.

The *testes*, which are often surrounded by eggs and therefore not easily seen, lie obliquely or symmetrically either side of the proximal female complex and often overlap the posterior border of the ventral sucker. They are oval, normally slightly smaller than the ovary and may lie contiguous to the vitelline masses. The vas deferens was not seen. Two types of *cirrus-sac* were seen:

(1) In *Diplodus annularis* the cirrus-sac is short, straight or slightly curved and slants posteriorly at an acute angle (Fig. 4C). The bipartite seminal vesicle has a larger proximal section and leads into a vesicular pars prostatica lined with globule-like anuclear bodies. Numerous glandular prostatic cells surround the pars prostatica and the straight ejaculatory duct and tend to obscure their details.

(2) In *Symphodus tinca* and *Sillago* spp. the cirrus-sac is long and strongly reflexed and overlaps the ventral sucker to a much greater degree than is seen in the specimens from *D. annularis* (Fig. 4B). The bipartite seminal vesicle has subequal, globular portions and leads to a long pars prostatica which is particularly wide proximally. It is lined with globule-like anuclear bodies or villous filaments. It apparently reaches almost to the distal extremity of the cirrus-sac where it becomes a short, narrow ejaculatory duct which could not be precisely delineated. The cirrus-sac also contains numerous gland-cells.

In both cases the ejaculatory duct opens into a shallow genital atrium on the left margin of about the middle of the forebody.

The subglobular *ovary* lies dorsally to the posterior half of the ventral sucker in about the median line or slightly displaced to the right. The oviduct passes posteriorly from the ovary and receives the common viteline duct and the duct from both Laurer's canal and the seminal receptacle before

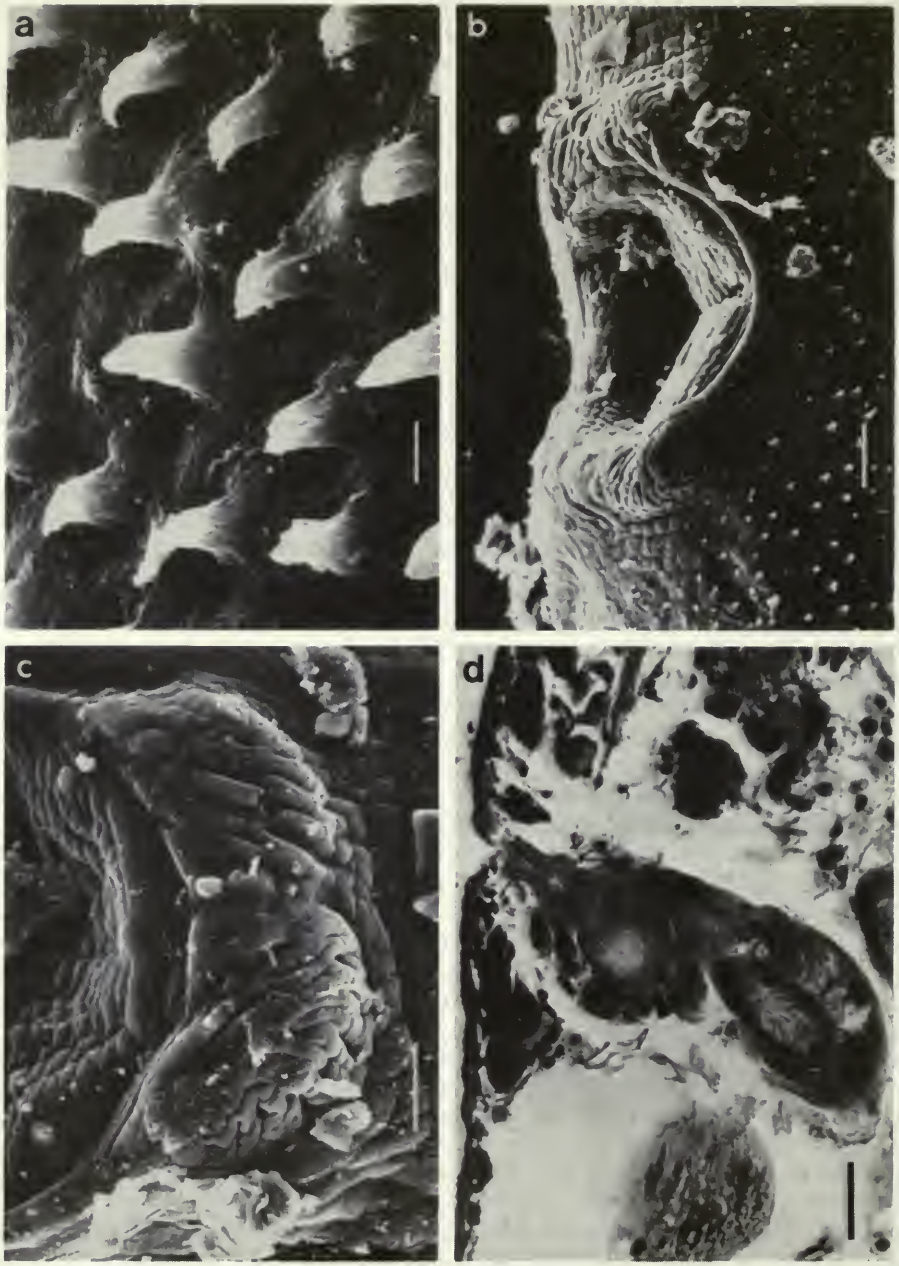


Fig. 3 *Diphterostomum brusinae* (Stossich), ex *Symphodus tinca*. (a) Tegumental spines in ventral forebody; (b) Lateral view of ventral sucker opening and lips; (c) Ventral sucker lip; (d) *Zoogonoides viviparus* (Olsson), photomicrograph of section showing atrial sac (arrowed). Scale bars: a 2 μm, b 20 μm, c 10 μm, d 30 μm.

entering Mehlis' gland. The small, sac-like, canalicular seminal receptacle is connected to the dorsal surface by a convoluted Laurer's canal which opens dorsally to one of the testes (Fig. 4D). The *uterus*, containing numerous eggs, fills much of the hindbody. The egg-capsules are very thin and in fixed specimens the eggs may appear to vary in size according to the medium in which they are mounted. In some preparations the egg-capsule appears completely membranous while in

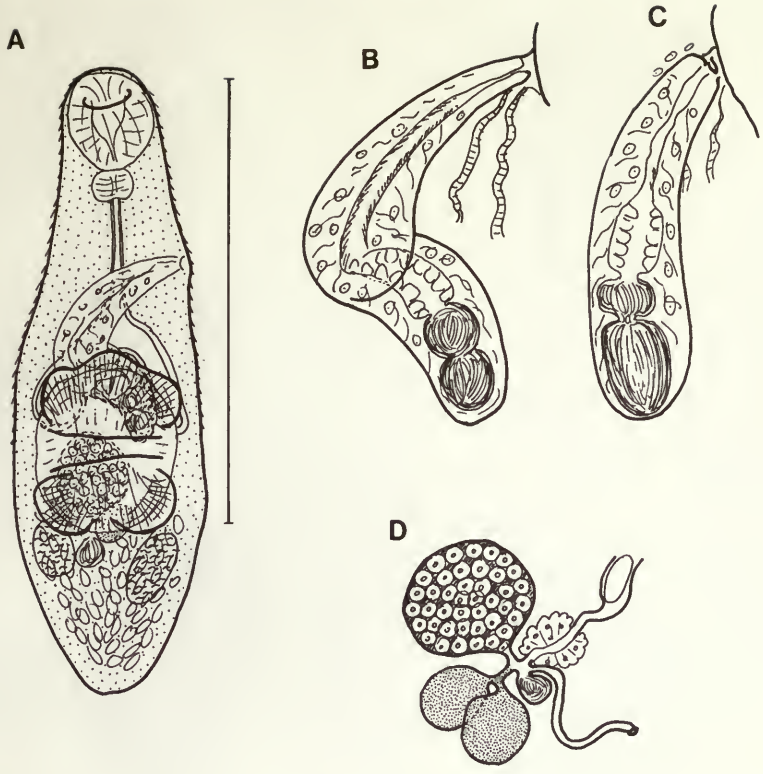


Fig. 4 *Diphterostomum brusinae* (Stossich). (A) ventral view, ex *Symphodus tinca*; (B) Cirrus-sac, ex *S. tinca*; (C) Cirrus-sac, ex *Diplodus annularis*; (D) Diagram of female proximal genitalia. Scale bar: A 0·5 mm.

others it appears, under certain optical conditions, to be *very* lightly tanned. The metraterm is wide and muscular in the *S. tinca* and *Sillago* spp. specimens and is much less so in *D. annularis*. The *vitellarium* consists of two subglobular masses which lie either side of the ovary and are connected by a broad isthmus from which the common vitelline duct leads.

Discussion. The two distinct forms of terminal genitalia described above indicate that two species may be present. We have not, however, separated these forms for a number of reasons.

(1) The literature, in particular Palombi (1930), shows a wide variation in the form of the cirrus-sac. In Palombi's paper the cirrus-sac is figured in a variety of forms and the figure (table 1, fig. 1) which shows the longest, most reflexed cirrus-sac is of a specimen from *Diplodus vulgaris*, a fish congeneric with the host of our 'short cirrus-sac' form '(1)'. Some figures in the literature (e.g. Looss, 1901) show an intermediate form, but in our, admittedly limited, material there is no evidence of an intermediate form.

(2) Our studies of the species *Pseudozoogonoides subaequiporus* (see below, p. 147) indicate that the cirrus-sac varies in form in a similar way to that postulated here for *D. brusinae*.

(3) It is difficult to be certain from Stossich's (1889) figure to which form the type-specimens belong.

(4) This species has been recorded, as such, only once in the north-east Atlantic and we have no specimens from this region.

It is clear, however, that the structure of the cirrus-sac needs more careful study in this species. Further studies of material from the Mediterranean basin may show that more than one species has been confused, and this may account for the variation apparently found in the life-cycle.

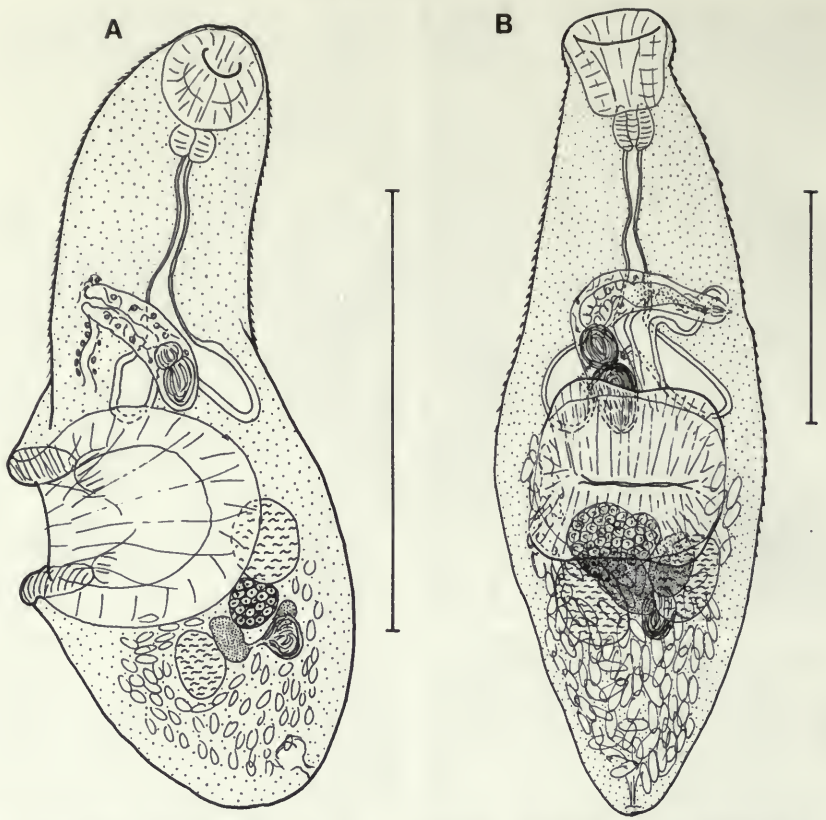


Fig. 5 *Diphterostomum brusinae* (Stossich). (A) Sublateral view, ex *Diplodus annularis*; (B) Ventral view, ex *Sillago maculata*. Scale bars: A 0·5 mm, B 0·2 mm.

The specimens from *Sillago* occasionally show a slightly infundibuliform terminal oral sucker (Fig. 5B), but not invariably. The eggs in these specimens also tend to be smaller than the Mediterranean form.

Diphterostomum sargus annularis Vlasenko, 1931, from *Diplodus annularis* in the Black Sea has been considered a synonym of *Diphterostomum brusinae* by Dolgikh & Naidenova (1967), and this seems acceptable as no differences between it and the generalized form the *D. brusinae* which we describe can be found. This also applies to *D. spari* Yamaguti, 1938, of Ergens (1960), who described his form from *Diplodus vulgaris* off Albania. We are inclined to consider that Yamaguti's original single specimen of *D. spari*, from *Sparus longispinus* in Japan, belongs to *D. brusinae*. He distinguished this species on egg-size (about 60×24 μm), but this single measurement indicates that he measured only one or a few eggs. The egg-capsule is very thin and we have found that specimens mounted in Canada balsam show an egg-size distinct from those mounted in glycerine jelly, so it appears that this character should be used with caution in this group. Published measurements of *D. brusinae* approach those quoted for *D. spari*.

Diphterostomum macrosaccum Montgomery, 1957, from the 'cardiac end of stomach' of *Neoclinus uninotatus* from California appears to be a typical example of the long cirrus-sac form of *D. brusinae*. The genital pore is said to be dorsal, but is close to the lateral margin and is not readily distinguishable from the lateral pore of *D. brusinae*. This is, therefore, the first record of *D. brusinae* from the western coast of the USA although it has previously been recorded in the north Pacific by Yamaguti (1934, 1938) from Japan.

Diphterostomum anisotremi Nahhas & Cable, 1964, from pomadasyid fishes off Florida, Jamaica, Venezuela, southern Brazil and Ghana is herein considered a synonym of *D. brusinae*.

Table 3 Measurements of *Diphterostomum brusinae*

Authority	Fischtal (1980)	Present study		
Name used	*Diphterostomum israelense*	*Diphterostomum brusinae*		
Host	*Diplodus* spp. *Saurida*	*Crenilabrus tinca*	*Diplodus annularis*	*Sillago* spp.
Locality	Israel	Yugoslavia	Yugoslavia	Queensland
Length (mm)	0·73–1·18	0·63–0·81	0·84–1·0	0·60–0·70
Breadth (mm)	0·17–0·26	0·21–0·28	0·27	0·15–0·24
Length : forebody ratio	[1 : 0·53–0·55]	1 : 0·48–0·53	1 : 0·43–0·52	1 : 0·35–0·50
Oral sucker (mm)	0·09–0·12 × 0·09–0·13	0·10–0·11 × 0·10–0·12	0·12 × 0·09–0·12	0·09–0·10 × 0·06–0·09
Ventral sucker (mm)	0·16–0·23 × 0·14–0·20	0·18–0·21 × 0·15–0·18	0·18 × 0·20	0·14–0·15 × 0·13–0·17
Sucker-ratio				
width	1 : 1·42–1·61	1 : 1·50–1·54	1 : 1·67	1 : 1·4–2·0
length	1 : 1·62–1·90	1 : 1·62–2·08	1 : 1·50–2·34	
Pharynx (mm)	0·034–0·048 × 0·032–0·049	0·04–0·05 diam.	0·04–0·05 diam.	0·04–0·05 × 0·03–0·04
Oesophagus (mm)	0·22–0·35	0·13–0·17	0·125–0·25	0·07–0·11
Cirrus-sac (mm)	crescent 0·20–0·30 × 0·04–0·075	recurved 0·16–0·20 + 0·14–0·15 × 0·05–0·06	straight 0·15–0·20 × 0·06–0·07	0·15–0·24 × 0·04–0·045
Testes (mm)	0·06–0·07 × 0·085–0·11	–	0·08–0·11 × 0·06–0·08	0·07–0·10 × 0·04–0·06
Ovary (mm)	0·07–0·10 × 0·07–0·09	0·09–0·10 × 0·08–0·09	0·12 × 0·09	0·04–0·06 diam.
Eggs (μm)	33–44 × 13–18	30–45 × 15–24	35–39 × 12–18	28–31 × 9–11

The sucker is obviously strongly muscular although the lips were not originally described, and in the specimen figured in the original description the sucker has taken up a lateral configuration which often happens in *D. brusinae* (see Fig. 5A). Amato's (1983) description, however, stressed the muscular 'flap-like' extensions of the ventral sucker. The sucker ratios quoted by Nahhas & Cable (1964) and Amato (1983) are 1 : 2–2·35 and 1 : 2·06–2·47, respectively, which appear to be slightly more than is usual for *D. brusinae*. Fischthal & Thomas (1968) quoted the figures 1 : 1·46–2·0 when recording this parasite from *Pomadasys jubelini* off Ghana. It should be noted that this fish in the south-east Atlantic has been recorded as a host of *D. brusinae* by Aleshkina (1979).

Diphterostomum tropicum Durio & Manter, 1968, recorded from *Lethrinus* sp., New Caledonia, *L. glyphodon,* Queensland, Australia (Durio & Manter, 1968) and *Chrysophrys auratus,* New Zealand (Korotaeva, 1975) is herein considered a synonym of *D. brusinae*. Examination of the holotype (USNM 63308) has shown that muscular lamellar lips are present on the ventral sucker, so the major point of difference reported by Durio & Manter appears to be invalid. The other differentiating features invoked by Durio & Manter do not appear to differ from those exhibited by *D. brusinae* as described above.

Diphterostomum israelense Fischthal, 1980, from *Diplodus sargus*, *D. annularis* and *Saurida undosquamis* from the Israeli coast of the Mediterranean, is not distinguishable from *D. brusinae*. The variations in this species which we described above comfortably encompass Fischthal's (1980) description, and *D. annularis* is one of the hosts from which our material was recovered.

Diphterostomum betencourti (Monticelli, 1893) Odhner, 1911

Distomum betencourti Monticelli, 1893.
Pleurogenes betencourti (Monticelli, 1893) Stossich, 1899.
Distoma lutea van Beneden, 1871 *nec* von Baer, 1857.
Brachycoelium luteum (van Beneden, 1871) Giard, 1897.
Diphterostomum luteum (van Beneden, 1871) Stossich, 1903.
Distomum (Brachycoelium) luteum (van Beneden, 1871) Giard, 1907.

TYPE-HOST AND LOCALITY. *Scyliorhinus caniculus*, Belgian coast.

RECORDS

(i) Material studied
(a) From the NE Atlantic

Scyliorhinus caniculus [spiral intestine] Roscoff, Finistère, France (Sept. 1938). Collected by O. Nybelin. Lent by Goteborgs Naturhistoriska Museet.
Scyliorhinus stellaris [spiral intestine] Roscoff, Finistère, France (Sept. 1938). Collected by O. Nybelin. Lent by Goteborgs Naturhistoriska Museet.

(b) From elsewhere
None

(ii) NE Atlantic records from the literature
(?) *Chelon labrosus* [intestine] Ostende, Belgium. van Beneden (1871: 28; as *Distoma luteum*, 'Elles ressembles beaucoup à un Distoma que nous avons vu dans le *Scillium canicula*').
Scyliorhinus caniculus [intestine] Belgian coast. van Beneden (1871: 3; as *Distoma lutea*).
—— [rectum] Saint Serran, Ille-et-Vilaine, France. Dollfus (1937: 60).
—— [rectum] Roscoff, Finistère, France. Dollfus (1937: 60).
—— [spiral intestine] Roscoff, Finistère, France. Sproston (1939: 37).
Scyliorhinus stellaris [?] Wimereux, Artois, France. Monticelli (1890: 424; as *Distomum luteum*); Odhner (1911*a*: 242).
—— [stomach] Boulogne, Artois, France. Dollfus (1937: 61).

ASPECTS OF BIOLOGY. This species, along with *Pseudozoogonoides* sp. innom., is among the few zoogonids described from elasmobranchs. In contrast to the third zoogonid species from elasmobranchs, *Steganoderma (Steganoderma) formosum*, reported as an accidental parasite of *Squalus acanthias* and *Raja naevus* by Myers (1959) and Threlfall (1969), this species appears to inhabit these dogfish as its preferred hosts. The above records are, we believe, a complete list of the records of this species. It is, therefore, reported from a very restricted area.

No details of the life-history are known.

PREVIOUS DESCRIPTIONS. van Beneden (1871: plate IV fig. 9; as *Distoma lutea*); Monticelli (1890: 424; as *Distomum luteum*); Stossich (1903: 193; as *Distomum betencourti*); Odhner (1911*a*: 242).

DESCRIPTION (Fig. 6). Five specimens from *S. caniculus* and two from *S. stellaris* were examined in flattened whole-mount preparations (Fig. 6). The measurements are given on Table 4. The body is oval in outline and bears spines back to about the level of the ventral sucker. The subglobular *oral sucker* opens subterminally, and leads via a small prepharynx, or sometimes apparently directly, into a small globular *pharynx*. The distinct oesophagus varies considerably in length and bifurcates in the posterior half of the forebody, giving rise to short caeca which reach to about the middle of the ventral sucker, abutting the anterior edge of the testes. They are normally bulbous, but may appear narrow. The *ventral sucker* is larger than the oral, but does not bear the conspicuous muscular lips of *D. brusinae*. It is transversely elongate, lying in the posterior half of the body.

The *excretory pore* is terminal. The details of the vesicle were not seen, but in some worms a large, bulbous vesicle can be seen posteriorly to the uterine field.

The oval *testes* usually lie with their long axis orientated longitudinally in a symmetrical to oblique configuration to either side of the anterior, middle or occasionally posterior region of the ventral sucker. The long *cirrus-sac* reaches to a point between a level just posterior to the anterior margin of the ventral sucker and a level just posterior to the ventral sucker. It is usually more or less

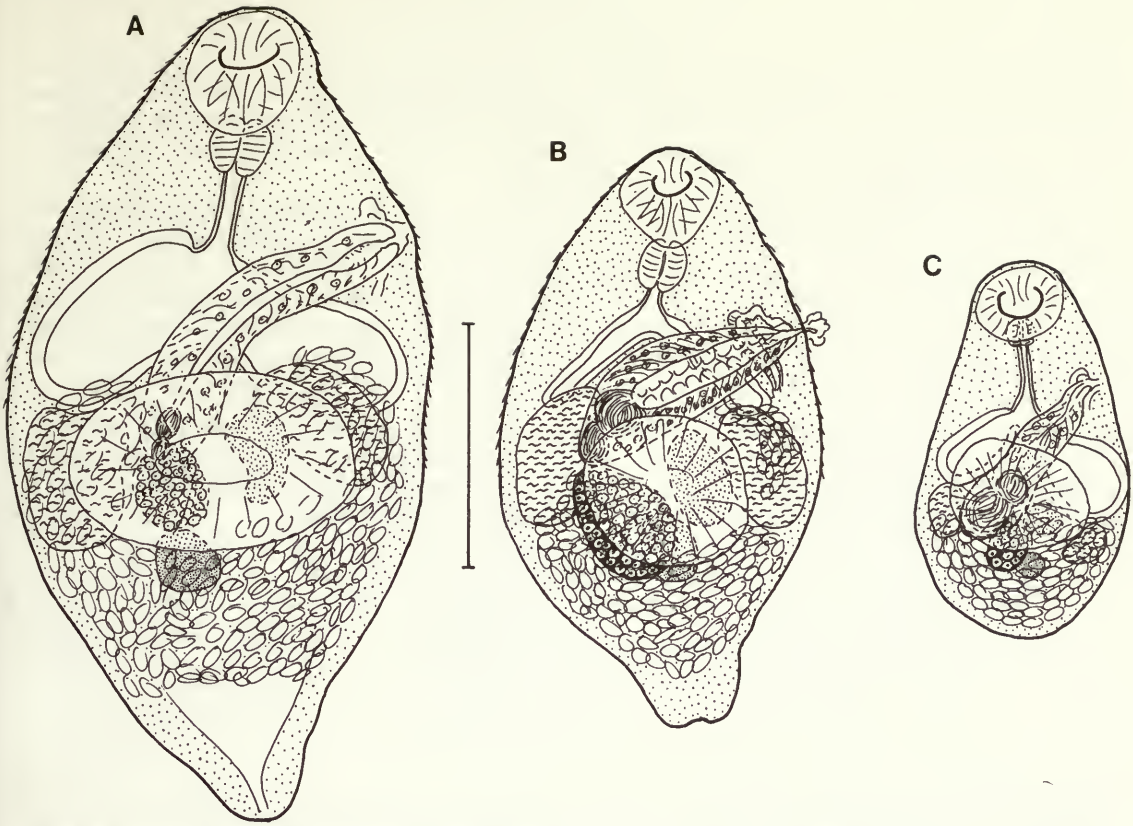


Fig. 6 *Diphterostomum betencourti* (Monticelli). (A), (B) Flattened specimens, ex *Scyliorhinus caniculus*; (C) Flattened specimen, ex *Scyliorhinus stellaris*. Scale bars: A, B, C 0·5 mm.

Table 4 Measurements of *Diphterostomum betencourti*

Authority	Odhner (1911*a*)	Present study	
Host	*S. stellaris*	*S. caniculus*	*S. stellaris*
Length (mm)	2–2·5	0·81–1·62	0·69–0·75
Breadth (mm)	1·1–1·3	0·41–0·85	0·43–0·44
Length : forebody ratio	–	1 : 0·44–0·51	1 : 0·43–0·51
Oral sucker (mm)	0·3 diam.	0·16–0·25 × 0·17–0·25	0·15–0·17 × 0·17–0·18
Ventral sucker (mm)	0·43 × 0·60–0·65	0·10–0·32 × 0·27–0·55	0·19–0·20 × 0·29–0·28
Sucker-ratio	–	1 : 1·5–2·3	1 : 1·6
Pharynx (mm)	0·24	0·07–0·11 × 0·06–0·12	0·08 diam.
Oesophagus (mm)	–	0·06–0·18	0·06–0·17
Cirrus-sac (mm)	–	0·30–0·78 × 0·08–0·18	0·40–0·41 × 0·10
Testes (mm)	–	0·12–0·30 × 0·07–0·20	0·17–0·18 × 0·10–0·12
Ovary (mm)	–	0·11–0·20 × 0·06–0·15	–
Eggs (μm)	34–36 long	30–34 × 13–16	31–32 × 15–16

straight, but may be twisted distally. A bipartite seminal vesicle, which varies in size, is contained within the cirrus-sac along with a long wide pars prostatica lined with cell-like blebs and filaments and surrounded by gland-cells and a muscular ejaculatory duct which may occasionally be everted to form an irregularly lobed cirrus (Fig. 6B). A small, distinct genital atrium occurs. The genital pore lies on the left lateral margin of the mid-forebody.

As only flattened whole-mounts were available for study, some details of the female system were not seen. The oval *ovary* lies dorsally to the posterior edge of the ventral sucker or in that vicinity. The seminal receptacle and Laurer's canal were not seen. The egg-shells are thin, but apparently very lightly tanned, and are mostly collapsed, and the *uterus* occupies much of the hindbody. The muscular metraterm loops anteriorly to the distal end of the cirrus-sac and enters the genital atrium via its anterior wall. Two large subglobular masses form the *vitellarium,* which lies dorsally or posteriorly to the ventral sucker, the lobes lying in either an oblique or a tandem arrangement.

DISCUSSION. This species is poorly known. Monticelli (1893) replaced the preoccupied name *Distoma lutea* van Beneden, 1871, with *D. betencourti.* No full description, with adequate metric data, has previously been presented. *Cercaria lutea* (van Beneden) of Giard (1897) is probably a synonym of *Bacciger bacciger* (Rudolphi, 1819) (see Bray & Gibson, 1980).

Diphterostomum vividum (Nicoll, 1912) n. comb.

Zoonogenus vividus Nicoll, 1912.
Zoogonoides vividus (Nicoll, 1912) Yamaguti, 1953.

TYPE-HOST AND LOCALITY. *Pagellus bogaraveo,* Aberdeen.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Pagellus bogaraveo [rectum] Plymouth, Devon, England (Oct. 1972). BM(NH) 1982.5.4.1–3.

(b) From elsewhere
None

(ii) NE Atlantic records from the literature
Pagellus bogaraveo [rectum] Aberdeen, Scotland. Nicoll (1912: 200; 1913: 189).
—— [rectum] Plymouth, Devon, England. Nicoll (1912: 200; 1913: 189).

ASPECTS OF BIOLOGY. This species is little known. It has only been recorded from the rectum of *P. bogaraveo* in the two localities mentioned above.

PREVIOUS DESCRIPTIONS. Nicoll (1912: 200).

DESCRIPTION (Fig. 7A,B). Five specimens, two as both whole-mounts and serial sections, have been studied. The measurements are included in Table 5. These oval worms have transverse rows of tegumental spines which reach back to about the level of the middle of the ventral sucker. The *oral sucker* may be terminal and slightly infundibuliform or more or less globular with a subterminal opening. A short prepharynx leads via a small, globular *pharynx* to a distinct oesphagus which bifurcates in the mid to posterior forebody region. The caeca reach no further posteriorly than the middle of the ventral sucker. In about the middle of the body a large, subcircular *ventral sucker* is found, without a strongly developed musculature.

The *excretory pore* is terminal, leading into a small sac-like vesicle, often containing acinous crystalline structures.

The *testes,* which are not clearly seen in whole-mounted worms, lie symmetrically to slightly obliquely close to the posterior margin of the ventral sucker. They are mainly post-ovarian and lie contiguous with the vitelline masses. The large, recurved *cirrus-sac* reaches dorsally to the ventral sucker (Fig. 7A,B). The proximal part contains a bipartite seminal vesicle and part of a wide pars prostatica. The distal part runs transversely and contains the remainder of the pars prostatica and a short ejaculatory duct which may be extended to form a cirrus. The small genital atrium opens on the left lateral margin at about the level of the intestinal bifurcation.

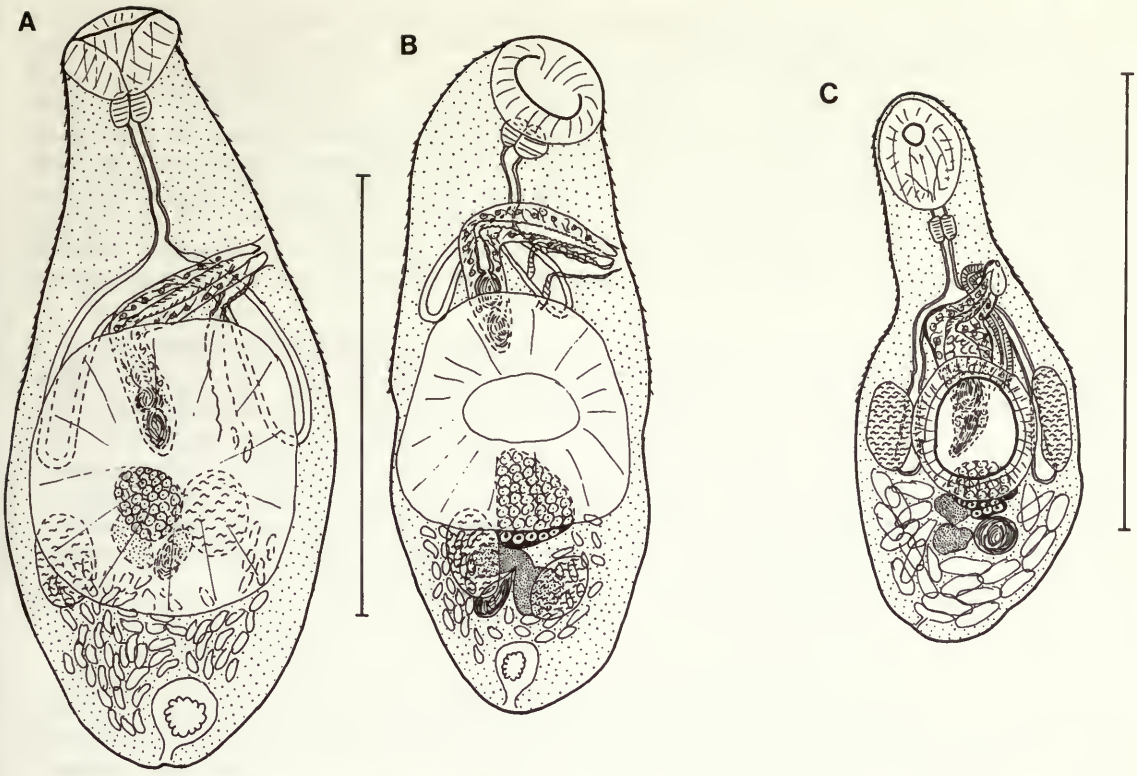


Fig. 7 (A), (B) *Diphterostomum vividum* (Nicoll), Ventral views; (C) *Pseudozoogonoides* sp. innom., ex *Squalus acanthias*, ventral view. Scale bars: A, B, C 0·5 mm.

Table 5 Measurements of *Diphterostomum vividum* and *Pseudozoogonoides* sp. innom.

Authority	*Diphterostomum vividum* Nicoll (1912)	*Diphterostomum vividum* Present study	*Pseudozoogonoides* sp. innom. Present study
Length (mm)	av. 1·4	0·80–0·84	0·59
Breadth (mm)	av. 0·46	0·32–0·37	0·25
Length : forebody ratio	[1 : 0·50]	1 : 0·32–0·37	1 : 0·49
Oral sucker (mm)	*c.* 0·16 diam.	0·10 × 0·13	0·11 × 0·08
Ventral sucker (mm)	*c.* 0·34 diam.	0·30–0·33 × 0·30	0·15 × 0·13
Sucker-ratio	*		
width		1 : 2·3	1 : 1·6
length		1 : 2·08–3·3	1 : 1·4
Pharynx (mm)	0·07 diam.	0·05–0·06 diam.	0·32 × 0·27
Oesophagus (mm)	'shorter than pharynx'	0·13 × 0·14	0·07
Cirrus-sac (mm)	–	0·36–0·41 × 0·05	0·24 × 0·06
Testes (mm)	*c.* 0·25 × 0·12	–	0·10–0·11 × 0·05
Ovary (mm)	0·09	–	0·075 × 0·05
Eggs (μm)	16–36 × 12–18	31–39 × 12–19	45–55 × 14–25

*Ventral sucker 'distinctly more than twice [size] of oral sucker and in some cases it is nearly three times.'

The subglobular *ovary* overlaps the posterior margin of the ventral sucker. The elements of the female system are closely packed making interpretation of details difficult. The oviduct appears to pass posteriorly from the ovary and receives Laurer's canal, which passes anteriorly and opens dorsally at about the mid-level of the ovary. Posteriorly to the ovary and vitellarium is the ampullaceous seminal receptacle with a duct whose full course could not be traced. An amorphous Mehlis' gland apparently lies in about the median line at roughly the level of the seminal receptacle. The *uterus*, which occupies much of the hindbody, contains small eggs with thin membranous capsules. Dorsally to about the middle of the ventral sucker the uterus forms a wide, muscular metraterm which enters the genital atrium through a narrow opening in its posterior wall. The *vitellarium* consists of two masses joined by a broad isthmus from which the common duct passes into the oviduct.

Discussion. The major discrepancy between our observations and those of Nicoll (1912) concerns the nature of the vitellarium. Nicoll described it as 'a small compact mass lying near the ovary, sometimes on its right side, sometimes behind it'. In none of our whole-mounts could the vitellarium be adequately observed. Perhaps Nicoll had similar problems. He also stated that 'the parasites were usually in a more or less macerated condition'. Our observations indicate that this species should be included in the genus *Diphterostomum* and differs from *D. brusinae* in the size and nature of the ventral sucker. In the few specimens of *D. vividum* we have available we were unable to see muscular, lamellar lips on the ventral sucker. Both the sucker-width and sucker-length ratios of *D. vividum* exceed those of *D. brusinae* with no overlap (see Tables 3 and 5).

Genus ***PSEUDOZOOGONOIDES*** Zhukov 1957

Diagnostic features. Ventral sucker in middle of body; usually subequal to slightly or distinctly larger than oral sucker. No muscular lamellar lips. Oesophagus distinct, bifurcates in forebody. Caeca narrow, just reach into hindbody. Testes symmetrical at level of ventral sucker. Cirrus-sac variable. Seminal vesicle bipartite. Pars prostatica vesicular. Genital atrium distinct, with atrial sac. Genital pore marginal, sinistral; in mid-forebody. Ovary subglobular, post-testicular. Vitellarium two subequal masses. Uterus fills most of hindbody. Miracidium surrounded by membranous or very weakly tanned egg-capsule. Excretory pore terminal, vesicle small, saccular. (? Metacercaria in teleosts.) Adults in teleosts and elasmobranchs.

Comment. Zhukov (1957) distinguished the genus *Pseudozoogonoides* from *Diphterostomum* on the structure of the ventral sucker, which in the latter genus has strongly muscular lamellar lips. To some extent it is a matter of personal preference whether this single character is considered to be of generic importance, but it is suggested (Bray, in press *a*) that *Pseudozoogonoides* should be retained for those zoogonines with two vitelline masses, relatively narrow elongate caeca and an atrial sac. Skrjabin (1957) referred to Zhukov's unpublished dissertation and mentioned two possible further differentiating features. These are: (1) that *Diphterostomum* is a southern form while *Pseudozoogonoides* is northern, and (2) the known details of the life-cycle are different, in that the metacercariae of *P. microacetabulum* (= *subaequiporus*) are said to occur in a fish.

The genus *Pseudozoogonoides* has been credited with two further species, *P. ugui* Shimazu, 1974, from the posterior intestine of the cyprinid *Tribolodon hakonesis* from inshore waters and a river in Japan, and *P. albulae* (Overstreet, 1969) Madhavi, 1979 from the intestine and pyloric caeca of *Albula vulpes* from Florida. *P. albulae* was originally placed in *Diphterostomum* and is considered a member of that genus.

Key to *Pseudozoogonoides* spp. found in the north-east Atlantic

1 Sucker ratio 1 : < 1·2; parasite of teleosts . . . . *P. subaequiporus* (Odhner, 1911) (p. 147)
— Sucker ratio 1 : > 1·2; parasite of elasmobranchs . . . . . *P.* sp. innom. (p. 150)

Pseudozoogonoides subaequiporus (Odhner, 1911) n. comb.

Zoogonoides subaequiporus Odhner, 1911.
Diphterostomum microacetabulum Shulman-Albova, 1952.
Pseudozoogonoides microacetabulum (Shulman-Albova, 1952) Zhukov, 1957.
Zoogonoides viviparus of Scott (1973, 1975*a*,*b*).
(?) *Diphterostomum* sp. of Brinkmann (1975).

TYPE-HOST AND LOCALITY. *Anarhichas lupus*, Trondheim, Norway.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Anarhichas lupus [intestine, posterior intestine] off NE Scotland (58°N, 00°; depth 99–111 m; and 59°N, 01°E; depth 107–117 m; Dec. 1979) BM(NH) 1982.4.21.13–16; Bell Rock, North Sea (56°N, 02°W; depth 52 m; May 1982) BM(NH) 1983.11.23.17–18; W of Bressay Bank (59°N, 00°; depth 140 m; June 1983) BM(NH) 1983.11.23.17–18.
Anarhichas minor [intestine] Anton Dohrn Bank, E, Greenland (66°N, 30°W; depth 336–380 m; May 1973) BM(NH) 1982.4.21.17–19.
Hippoglossoides platessoides [intestine] Latragrunn, W. Iceland (66°N, 27°W; depth 216–228 m; May 1973) BM(NH) 1982.4.21.20.
Lycodes esmarkii [intestine] Foula, Scotland (60°N, 06°W; depth 800 m; June 1974) BM(NH) 1982.4.21.21.

(b) From elsewhere
Hippoglossoides platessoides [intestine] off Newfoundland and Nova Scotia, Canada (see Bray, 1979: 417; as *D. microacetabulum*). BM(NH) 1977.2.15.54–58

(ii) NE Atlantic records from the literature
Anarhichas lupus [posterior intestine] Trondheim, Norway (1905). Odhner (1911*a*: 244).
(?) *Anarhichas minor* [gall-bladder] Off Umîvik, E. Greenland (July, 1959). Brinkmann (1975: 40; as *Diphterostomum* sp.).

ASPECTS OF BIOLOGY. The life-history of this worm is not known in any detail. The miracidium, which bears a dense coat of cilia, is enclosed by a thin membranous capsule, but according to Shulman-Albova (1952) hatches and swims freely in the host's intestine. There appears to be a direct relationship between 'viviparity' and the situation in the posterior part of the gut. The host of the sporocyst generations is not known. *Cercaria zoogonoides* Chubrik, 1966 from the gastropods *Buccinum finmarchianum* and *Sipho islandicus* from the Barents Sea could represent this species or possibly *Zoogonoides viviparus*. Shulman-Albova (1952), drawing a parallel with *Diphterostomum brusinae*, speculated that gastropods of the genus *Natica* constitute the first intermediate hosts and that the definitive host (*Anarhichas* in this case) gains the parasite directly by feeding on these molluscs. The parallel with *D. brusinae*, however, may not be valid as we do not consider *Diphterostomum* and *Pseudozoogonoides* to be particularly closely related.

The only record of metacercariae is that of Zhukov (1960), who claimed to have found some in the mesenteries of the flatfish *Limanda punctatissima punctatissima* in the north Pacific Ocean. Scott's (1975*a*) studies suggested to him that brittle-stars were the second intermediate hosts of his *'Zoogonoides viviparus'* which he later (1982) re-identified as *Diphterostomum microacetabulum* [= *P. subaequiporus*].

The adult worm has been recorded in the north-east and north-west Atlantic, the White and Barents Seas and in various regions of the north Pacific. Most records are from pleuronectid flatfishes and anarhichadids, but cottids, zoarcids and salmonids are also recorded as hosts. In the north-west Atlantic, however, it apparently occurs only in *Hippoglossoides platessoides* and has been known under the name *'Zoogonoides viviparus'* in that region. As mentioned above, Scott (1982) corrected his earlier identifications (1973, 1975*a*,*b*) of worms from *H. platessoides*, and all the zoogonine worms we have recovered from this host in the north-west Atlantic (Bray, 1979) are *P. subaequiporus*.

PREVIOUS DESCRIPTIONS. Odhner (1911*a*: 244); Shulman-Albova (1952: 86; as *Diphterostomum microacetabulum*); Shulman & Shulman-Albova (1953: 46; as *D. microacetabulum*); Zhukov (1960:

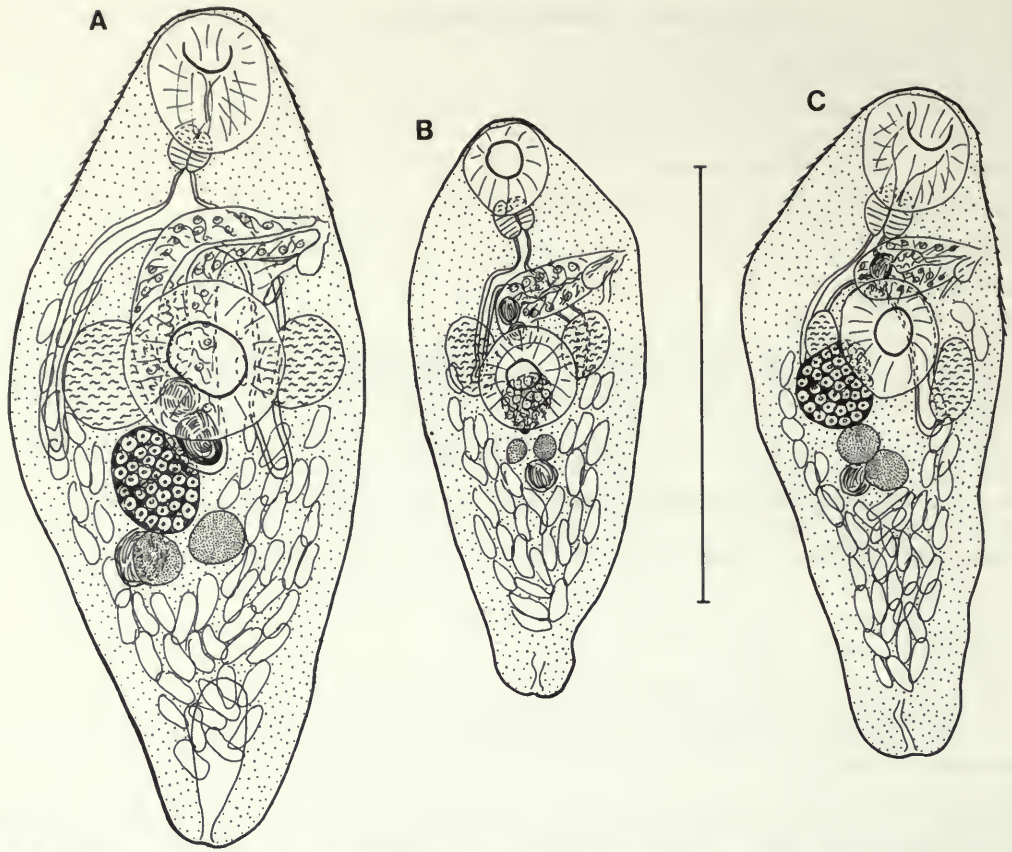


Fig. 8 *Pseudozoogonoides subaequiporus* (Odhner). (A) Ventral view, ex *Anarhichas lupus*, Scotland; (B) Ventral view, ex *Hippoglossoides platessoides*, Canada; (C) Ventral view, ex *Lycodes esmarkii*, Scotland. Scale bars: A, B, C 0·5 mm.

28; as *Pseudozoogonoides microacetabulum*); Brinkmann (1975: 38; as *D. microacetabulum* and (?) *Diphterostomum* sp.).

DESCRIPTION (Fig. 8). Forty-six whole-mounts and five sets of serial sections were examined. For measurements see Table 6. These small fusiform worms are normally widest in the forebody and may bear transverse rows of small, peg-like spines. The spines are more often than not apparently worn down, or at least not clearly seen. The subterminal *oral sucker* leads, via a short prepharynx, into a small, globular *pharynx*. The oesophagus divides in the mid-forebody region, giving rise to narrow caeca which terminate at about the level of the posterior margin of the ventral sucker or posterior margin of the testes, but this varies a little either anteriorly or posteriorly to that point. The subcircular ventral sucker is nearly always slightly larger than the oral.

The terminal *excretory pore* leads into an elongate, oval excretory vesicle which reaches almost half-way along the hindbody.

Oval *testes* lie almost symmetrically at the level of the ventral sucker, but occasionally one of the pair may be displaced into the forebody. The *cirrus-sac* is a variable structure and may be claviform and straight or distinctly recurved, i.e. formed of two parts: the distal part running almost transversely across the body and the proximal part running longitudinally. Intermediate forms occur (Fig. 8B) and, therefore, these differences cannot be considered as of taxonomic importance (see also *D. brusinae*, p. 139). The figures in Zhukov (1960) and Brinkmann (1975) show that this variation also occurs in other parts of the species' range. A seminal vesicle consisting of two oval parts lies proximally within the cirrus-sac. It leads into a wide, oval, vesicular pars prostatica, lined

Table 6 Measurements of *Pseudozoogonoides subaequiporus*

Host	*Anarhichas lupus*	*Anarhichas minor*	*Hippoglossoides platessoides*	*Lycodes esmarkii*
Length (mm)	0·81–0·96	0·65–0·69	0·67–1·04	0·76
Breadth (mm)	0·31–0·40	0·20	0·24–0·38	0·30
Length : forebody ratio	1 : 0·27–0·35	1 : 0·34–0·38	1 : 0·30–0·36	1 : 0·28
Oral sucker (mm)	0·15–0·16 × 0·15–0·17	0·12–0·13 × 0·11	0·09–0·18 × 0·09–0·12	0·13 × 0·12
Ventral sucker (mm)	0·17–0·18 × 0·15–0·18	0·12 × 0·11	0·10–0·16 × 0·10–0·14	0·14 × 0·12
Sucker-ratio	1 : 1·0–1·2	1 : 0·98	1 : 1·0–1·3	1 : 1·0
Pharynx (mm)	0·05–0·055 diam.	0·034 diam.	0·040–0·055 × 0·045–0·055	0·05 × 0·055
Oesophagus (mm)	0·05	present?	0·02–0·075	?
Cirrus-sac (mm)	straight 0·35 recurved* (A) 0·22–0·23 (B) 0·22–0·25 × 0·035–0·08	0·22 × 0·05	straight 0·18–0·34 recurved* (A) 0·14–0·28 (B) 0·07–0·19 × 0·05–0·08	0·15 × 0·05
Testes (mm)	0·11–0·15 × 0·09–0·11	0·08–0·09 × 0·05	0·08–0·11 × 0·04–0·09	0·06–0·09 × 0·05–0·06
Ovary (mm)	0·13 × 0·10–0·11	0·07 × 0·06	0·06–0·10 × 0·05–0·10	0·08 × 0·10
Miracidium (μm)	67–80 × 27–32	55–62 × 20	62–70 × 25	53–57 × 22–23

*Recurved cirrus-sac length measured in two parts: (A) distal part, (B) proximal part.

with cell-like, but apparently anuclear, structures and surrounded by glandular cells and connective tissue. Distally the pars prostatica narrows to form the ejaculatory duct, which opens into the base of the genital atrium. A small sac-like diverticle arises from the posterior margin of the genital atrium. The genital pore opens on the left margin of the mid-forebody or just ventrally sublateral.

The oval *ovary* lies on about the median line, overlapping the posterior border of the ventral sucker. From the ovary the oviduct passes posteriorly and receives the ducts from the seminal receptacle and Laurer's canal, close together, and the common vitelline duct. The seminal receptacle is variable in size, but is often a large, globular structure. A narrow Laurer's canal arises close to the opening of the seminal receptacle into the oviduct, so close in fact that it may be interpreted as a common opening, and passes dorsally to open on the surface dorsally to the seminal receptacle. Mehlis' gland is inconspicuous, lying, as far as can be ascertained, just anterior to the vitellarium. The *uterus* occupies much of the hindbody and contains numerous fairly large eggs with very thin capsules with little or no sign of tanning. The metraterm is wide and muscular, surrounded by gland-cells and opens into the base of the genital atrium. The *vitellarium* consists of two compact masses which are connected by a broad isthmus which feeds the oviduct through a common duct.

Discussion. This species is best known under the names *Diphterostomum* and *Pseudozoogonoides microacetabulum*, but, as such, has never been recorded in the north-east Atlantic. We have found it on a number of occasions, including two where it was sympatric with *Zoogonus rubellus*. Odhner (1911*a*) described briefly a form which he considered close to *Zoogonoides viviparus*, which he named *Zoogonoides subaequiporus* as the ventral sucker was much smaller. This characteristic fits closely with the present species, and, in fact, is the most convenient feature for initial differentiation

from *Z. viviparus*. The host Odhner mentions is *Anarhichas lupus*, which is also the type-host of *Diphterostomum microacetabulum*, originally reported from the White Sea. We have found specimens indistinguishable from *D. microacetabulum* from the same host in regions off north-east Scotland, and, therefore, it is likely that the distribution stretches from north Britain up the Norwegian coast to the Barents Sea (Polyansky, 1955) and the White Sea (Shulman-Albova, 1952; Shulman & Shulman-Albova, 1953). This part of this species' range includes Trondheim, the type-locality of *Z. subaequiporus*. Shulman-Albova (1952) considered it likely that *Z. subaequiporus* and *D. microacetabulum* were synonyms and the evidence presented by the discovery of this parasite fairly commonly in the north-east Atlantic region makes this likelihood so strong that we have taken the step of sinking *D. microacetabulum* into what is now *P. subaequiporus*.

The unnamed *Diphterostomum* sp. of Brinkmann (1975) from the gall-bladder of *Anarhichas minor* off east Greenland is very similar to *D. subaequiporus* and is, herein, tentatively considered a young representative of this species. The distinguishing features mentioned by Brinkmann should, however, be born in mind. He enumerates six, these are: (1) parasite of gall-bladder; (2) easily observed tegumental spines; (3) more posteriorly situated ventral sucker; (4) the wide, thin-walled intestinal caeca; (5) testes side by side level with, or posterior to ovary; and (6) large excretory vesicle. Some of these characters (2,3,5) may result from immaturity, while others (?4,6) may result from the different physiological regime encountered in the gall-bladder.

Pseudozoogonoides ugui differs from *P. subaequiporus* in having a relatively larger ventral sucker (sucker ratio 1 : 1·28–1·78) and larger eggs. The latter character is not a clear-cut one, as our measurements show that the egg-sizes reach into the range given by Shimazu (1974), and the egg-size in this subfamily tends to be somewhat unreliable. Two other distinguishing features mentioned by Shimazu are not valid, since the diverticulum of the genital atrium (atrial sac) is present in both species and the position of the genital pore is more or less identical.

Pseudozoogonoides sp. innom.

RECORDS

(i) Material studied

Squalus acanthias [spiral valve] Faxa Floi, S.W. Iceland (Oct. 1966) Collector: B. R. Manger. BM(NH) 1982.5.4.4.

ASPECTS OF BIOLOGY. Manger (1972) collected helminths from seven specimens of *S. acanthias* and 'some small, unidentified digenetic trematodes were found in the stomach and spiral valve'. Those from the stomach are *Derogenes varicus* (Müller, 1780), while the single specimen from the spiral valve is described below as *P.* sp. innom. The *Derogenes* are certainly accidental records in elasmobranchs (Threlfall, 1969; McVicar, 1977; Orlowska, 1980), but it is not possible to be certain if this is the case for *P.* sp. innom. Its location in the spiral valve and the known occurrence of the related worms in elasmobranchs (i.e. *D. betencourti*) indicate that *S. acanthias* may be a preferred host.

PREVIOUS DESCRIPTIONS.
None

DESCRIPTION (Fig. 7C). The single worm available is of a pyriform shape, widest in the region of the ventral sucker (Fig. 7C). The dimensions are given on Table 5. The spines on the body surface reach back as far as the ventral sucker with a patch on the ventral surface posterior to the ventral sucker. An oval *oral sucker* opens subterminally, leading via a distinct prepharynx into a small, oval *pharynx*. The long oesophagus reaches into the posterior forebody before bifurcating to form two narrow caeca which reach to about the posterior margin of the testes and the ventral sucker. The *ventral sucker* has a wide opening and a fairly narrow muscular wall, but it is distinctly larger than the oral sucker and lies just within the posterior half of the body.

The *excretory pore* is terminal and the vesicle, although not clearly seen, may be a small, flattened sac posterior to the uterine field.

The two oval *testes* lie, with their long axes longitudinal, on either side of the ventral sucker. The *cirrus-sac* is long and recurved, reaching almost to the ovary. It contains a bipartite seminal vesicle,

the distal part being globular and the proximal elongate–saccular. The pars prostatica forms a wide, oval vesicle and narrows distally where it is lined with filamentous structures. The cirrus-sac also contains numerous gland-cells. The ejaculatory duct opens into a distinct genital atrium with a small diverticulum (atrial sac). The genital pore lies on the ventral surface very close to the left margin of the body, in about the middle of the forebody.

The irregularly lobed *ovary* lies overlapping the posterior margin of the ventral sucker. A small, globular seminal receptacle lies to the left of the vitelline masses, immediately posterior to the ovary. The *uterus* occupies most of the posterior part of the worm and contains numerous large eggs, with thin, but apparently rigid, capsules. The metraterm is strongly muscular and runs from the hindbody towards the cirrus-sac over which it loops dorsally to enter the genital atrium from the anterior aspect. Two small, irregular *vitelline masses* lie in tandem postero-dextral to the ovary.

DISCUSSION. This single worm appears to differ from other described species of the genus, although from a single specimen no indication of intra-specific variation is possible. It differs from *P. subaequiporus* primarily in the sucker ratio, from the other species, *P. ugui* by egg-size, caeca and cirrus-sac length and from both species by its occurrence in an elasmobranch.

Genus ***ZOOGONOIDES*** Odhner, 1902

DIAGNOSTIC FEATURES. Prepharynx short. Oesophagus bifurcates in posterior forebody. Caeca narrow, reach close to testes or beyond. Cirrus-sac claviform with bipartite seminal vesicle. Distinct genital atrium with atrial sac usually present. Genital pore at or near lateral margin in mid-forebody. Ovary oval, post-testicular. Vitellarium single globular mass. Egg-capsules membranous. Sporocysts in gastropods. Tail-less xiphidiocercaria. Metacercaria in polychaetes, echinoderms, gastropods and bivalves. Adults in marine teleosts.

COMMENT. Only one species occurs in the north-east Atlantic.

Zoogonoides viviparus (Olsson, 1868) Odhner, 1902

Distoma viviparum Olsson, 1868.
Zoogonus viviparus (Olsson, 1868) Looss, 1901.
(?) *Distoma callionymi* van Beneden, 1871.
(?) *Cercaria megalocotylea* Villot, 1878.
Cercaria capriciosa Cuénot, 1892.
Cercaria giardi Pelseneer, 1906.
(?) *Cercaria limae* Nicoll & Small, 1909.
(?) *Metacercaria limae* (Nicoll & Small, 1909) James, Sannia & Bowers, 1977.

TYPE-HOST AND LOCALITY. *Microstomus kitt*, Bergen, Norway.

RECORDS

(i) Material studied
(a) From the NE Atlantic

Callionymus lyra [rectum, posterior intestine] Plymouth, Devon, England. Collector: M. Rothschild. BM(NH) 1932.11.22.43; and (May, 1972). BM(NH) 1982.3.4.13–20.
—— [intestine] off Myggenoes, Faeroe Bank (61°N, 09°W; depth 172–176 m; July, 1976). BM(NH) 1982.3.4.21.
—— [intestine] NNW Flannan Is., NW Scotland (58°N, 08°W; depth 116–120 m; July, 1976). BM(NH) 1982.3.4.22.
—— [intestine] W of Hoy Sound, Orkneys (60°N, 04°W; depth 96–97 m; July, 1976). BM(NH) 1982.3.4.23.
—— [intestine] off Wick, Moray Firth, Scotland (58°N, 03°W; depth 62–65 m; July, 1976). BM(NH) 1982.3.4.24–25.
—— [rectum, posterior intestine] northern North Sea (59°N, 04°W; depth 66 m; and 58°N, 03°W; depth 35 m; June, 1982). BM(NH) 1982.9.14.1–50.
Callionymus maculatus [posterior intestine, rectum] NE off Scotland (58°N, 02°W; depth 79–81 m; Dec., 1979). BM(NH) 1982.3.4.26.
Callionymus reticulatus [rectum, posterior intestine] Firth of Forth (56°N, 02°W; depth 60 m; May, 1982). BM(NH) 1982.9.14.51–55.

Glyptocephalus cynoglossus [intestine] NW Flannan Is., NW Scotland (59°N, 06°W; depth 106–108 m; July, 1976). BM(NH) 1982.3.4.27.

Gobius niger [posterior intestine, rectum] Crouch estuary, Essex, England. (May, 1980). BM(NH) 1982.3.4.28–29

Hippoglossoides platessoides [intestine, rectum] Aberdeen, Scotland. (Oct., 1973; March, 1977). BM(NH) 1982.3.4.30–33.

—— [intestine] Latragrunn, W of Iceland (66°N, 26°W; depth 248–250 m; May, 1973). BM(NH) 1982.3.4.34.; (65°N, 26°W; depth 110–208 m; May, 1974). BM(NH) 1982.3.4.35.

—— [rectum] Øresund, Helsingør, Denmark (Aug., 1981). BM(NH) 1982.3.4.36

—— [intestine, rectum] Firth of Forth (56°N, 02°W; depth 60 m; May, 1982). BM(NH) 1982.9.14.56–60.

—— [rectum] Alle Bank, North Sea (60°N, 03°E; depth 120 m; May, 1983). BM(NH) 1983.6.22.20.

Hippoglossus hippoglossus [rectum] SE Sule (59°N, 04°W; depth 55 m; June, 1982). BM(NH) 1982.9.14.61–62.

Lepidorhombus whiffiagonis [?] Off Aberdeen, Scotland. BM(NH) 1982.3.4.37–38.

Limanda limanda [intestine] 'Off Scottish coast'. Collector: Z. Kabata. BM(NH) 1964.6.23.4/25–28.

—— [posterior intestine] Plymouth, Devon, England. (May, 1972). BM(NH) 1982.3.4.39.

—— [rectum, intestine] Aberdeen, Scotland. (Oct., 1973) BM(NH) 1982.3.4.40–41.

—— [intestine] off Wick, Moray Firth, Scotland. (58°N, 02°W; depth 96–106 m; July, 1976). BM(NH) 1982.3.4.42.

—— [rectum, intestine] Kristineberg, Sweden. (Aug., 1976). BM(NH) 1982.3.4.43.

—— [rectum] Crouch estuary, Essex, England. BM(NH) 1982.3.4.44.

—— [intestine] Tromsø, Norway (June, 1980) BM(NH) 1982.3.4.45.

—— [rectum] Øresund, Helsingør, Denmark (Aug., (1981). BM(NH) 1982.3.4.46–48.

—— [posterior intestine, rectum] Montrose Bank, North Sea (56°N, 02°W; depth 50 m; May, 1982). BM(NH) 1982.9.14.63–80.

—— [rectum] Turbot Bank, North Sea (57°N, 01°W; depth 67 m; June, 1982). BM(NH) 1982.9.14.63–80.

—— [posterior intestine, rectum] Moray Firth (58°N, 03°W; depths 64 and 35 m; June, 1982). BM(NH) 1982.9.14.63–80.

Microchirus variegatus [intestine] off SW Ireland. (48°N, 09°W; depth 145–174 m; Jan., 1971). BM(NH) 1982.3.4.49.

—— [intestine] Bay of Biscay (44°N, 07°W; depth 272–280 m; Jan., 1971). BM(NH) 1982.3.4.50.

—— [intestine] NW of Flannan Is., NW Scotland. (59°N, 06°W; depth 106–108 m; July, 1976). BM(NH) 1982.3.4.51.

Microstomus kitt [rectum] Plymouth, Devon, England. (May, 1982). BM(NH) 1982.3.4.52.

—— [intestine] Aberdeen, Scotland. (Oct., 1973). BM(NH) 1982.3.4.53.

—— [rectum] Lossiemouth, Grampian, Scotland. (Oct., 1973). BM(NH) 1982.3.4.54.

—— [intestine] Faeroe Islands. (62°N, 08°W; depth 112 m; July, 1976). BM(NH) 1982.3.4.55.

—— [intestine] Moray Firth. (58°N, 02°W; depth 156 m; July, 1976). BM(NH) 1982.3.4.56.

—— [intestine] Øresund, Helsingør, Denmark. (Aug., 1981). BM(NH) 1982.3.4.88–89.

—— [posterior intestine, rectum] Moray Firth. (58°N, 03°W; depth 64 m; June, 1982). BM (NH) 1982.9.14.81.

Platichthys flesus [rectum] sea off Aberdeen. (Material of Gibson, 1972). BM(NH) 1972.3.27.15.; (Oct., 1973). BM(NH) 1982.3.4.57.

—— [rectum] Plymouth, Devon, England. (April, 1969). BM(NH) 1982.3.4.58.; (May, 1972). BM(NH) 1982.3.4.59–60.

Pleuronectes platessa [rectum] Plymouth, Devon, England. (May, 1932). Collector: H. A. Baylis. BM(NH) 1932.11.28.1–8; (May, 1972). BM(NH) 1982.3.4.61–63.

—— [intestine] off Scottish coast. Collector: Z. Kabata. BM(NH) 1964.6.23.5–24.

—— [intestine] Southern North Sea. Collector: J. F. Wickins. BM(NH) 1966.1.13.39–41.

—— [intestine] Faeroe Islands. (62°N, 08°W; depth 112–120 m; July, 1976). BM(NH) 1982.3.4.64.

—— [rectum] Kristineberg, Sweden. (Aug., 1977). BM(NH) 1982.3.4.65–66.

—— [intestine, rectum] Aberdeen, Scotland. (March, 1977). BM(NH) 1982.3.4.67.

—— [posterior intestine, rectum] Crouch estuary, Essex, England. (Sept., 1979). BM(NH) 1982.3.4.68–70.

—— [rectum] off Start Point, Devon, England. (March, 1980). BM(NH) 1982.3.4.71.

—— [rectum] Øresund, Helsingør, Denmark. (Aug., 1981). BM(NH) 1982.3.4.72–74.

—— [rectum] Swatchway, North Sea (58°N, 01°E; depth 84 m; June, 1982) BM(NH) 1982.2.9.82–85.

Pomatoschistus minutus [intestine, rectum] Crouch estuary, Essex, England. (Sept., Oct., 1979). BM(NH) 1982.3.4.75–77.

Solea vulgaris [rectum, intestine] Plymouth, Devon, England. (May, Oct., 1972). BM(NH) 1982.3.4.78–82.

—— [posterior intestine, rectum] Crouch estuary, Essex, England. BM(NH) 1982.3.4.83–85.

Zeus faber [intestine] Bay of Biscay. (45°N, 03°W; depth 132–280 m; Jan., 1971). BM(NH) 1982.3.4.86.
—— [rectum] Plymouth, Devon, England. (May, 1972) BM(NH) 1982.3.4.87.

(b) From elsewhere
None.

(ii) NE Atlantic records from the literature
Anarhichas lupus [rectum, intestine] St Andrews Bay, Scotland. Nicoll (1909: 16; 1914: 483).
Blennius gattorugine [rectum, intestine] Plymouth, Devon, England. Nicoll (1914: 483).
Blennius ocellaris [rectum] Plymouth, Devon, England. Nicoll (1914: 483).
Callionymus lyra [posterior intestine] Kristineberg, Sweden. Odhner (1902: 62).
—— [intestine] St Andrews Bay, Scotland. Nicoll (1909: 16).
—— [rectum] Millport, Firth of Clyde, Scotland. Nicoll (1910: 348).
—— [rectum] Plymouth, Devon, England. Nicoll (1914: 483); Baylis & Jones (1933: 630); Baylis (1939: 483).
(?) —— [intestine] Belgian coast, van Beneden (1871: 53; as *Distoma callionymi* – unrecognizable).
Glyptocephalus cynoglossus [rectum] North Sea. Nicoll (1909: 16).
—— [rectum] Aberdeen, Scotland. Nicoll (1913: 190).
Gobius niger [posterior intestine, rectum] Bergen, Norway. Køie (1976: 12).
Hippoglossoides platessoides [posterior intestine] Kristineberg, Sweden. Odhner (1902: 62).
—— [posterior intestine] Northumberland coast, England. Lebour (1908: 53).
—— [?] North Sea. Nicoll (1909: 16).
—— [rectum] Aberdeen, Scotland. Nicoll (1913: 190).
—— [posterior intestine] Øresund, Denmark. Køie (1976: 1).
Limanda limanda [posterior intestine] Kristineberg, Sweden. Odhner (1902: 62).
—— [rectum] St Andrews Bay, Scotland. Nicoll (1907: 83).
—— [posterior intestine] Northumberland coast, England. Lebour (1908: 53).
—— [rectum] Millport, Firth of Clyde, Scotland. Nicoll (1910: 348).
—— [rectum] Plymouth, Devon, England. Nicoll (1914: 483).
—— [rectum] Aberdeen, Scotland. Nicoll (1915: 360).
—— [rectum] Galway Bay, Ireland. Little (1929: 26).
—— [posterior intestine, rectum] Danish waters. Køie (1976: 1; 1981: 61; 1983: 215).
—— [posterior intestine, rectum] Faeroe Islands. Køie (1983: 215).
Microchirus variegatus [rectum, intestine] Plymouth, Devon, England. Nicoll (1914: 483).
Microstomus kitt [stomach] Bergen, Norway. Olsson (1868: 28).
—— [posterior intestine] Kristineberg, Sweden. Odhner (1902: 62).
—— [rectum] Firth of Clyde, Scotland. Nicoll (1909: 16; 1910: 348).
—— [rectum] Plymouth, Devon, England. Nicoll (1914: 483); Baylis & Jones (1933: 630); Baylis (1939: 483).
—— [?] St Andrews, Scotland. McIntosh (1926: 54).
Myoxocephalus scorpius [?] Molengrat, Texel, Netherlands. Willemse (1968: 85).
Platichthys flesus [posterior intestine] Kristineberg, Sweden. Odhner (1902: 62).
—— [rectum] Ythan estuary, Scotland. MacKenzie & Gibson (1970: 4); Gibson (1972: 6).
—— [rectum] Sea off Aberdeen. MacKenzie & Gibson (1970: 4); Gibson (1972: 6).
—— [rectum] Loch Ewe, Scotland. MacKenzie & Gibson (1970: 4).
—— [rectum] Dee estuary, Scotland. Gibson (1972: 6).
—— [posterior intestine, rectum] Øresund, Sweden. Køie (1976: 1).
—— [posterior intestine, rectum] Bergen, Norway. Køie(1976: 12).
—— [posterior intestine] SW coast of Sweden. Thulin (1981: 22).
Pleuronectes platessa [posterior intestine] Kristineberg, Sweden. Odhner (1902: 62).
—— [rectum] St Andrews, Scotland. Nicoll (1907: 83).
—— [posterior intestine] Northumberland coast, England. Lebour (1908: 53).
—— [posterior intestine] Luce Bay, Irish Sea (Oct., 1908). Johnstone (1909: 191).
—— [rectum] Millport, Firth of Clyde, Scotland. Nicoll (1910: 348).
—— [rectum] Plymouth, Devon, England. Nicoll (1914: 483); Baylis & Jones (1933: 630); Baylis (1939: 483); Dawes (1947: 245).
—— [rectum] Aberdeen, Scotland. Nicoll (1915: 360).
—— [intestine] Dale Fort, Dyfed, Wales. Crothers (1966: 23).
—— [rectum] Loch Ewe, Scotland. MacKenzie (1968: 13); MacKenzie & Gibson (1970: 4).
—— [rectum] Flamborough Head, German Bight and Southern Bight, North Sea. Wickins & Macfarlane (1973: 14).
—— [rectum] Øresund, Sweden. Køie (1976: 1).

Psetta maxima [rectum] St Andrews, Scotland. Nicoll (1907: 83).
Solea vulgaris [?] Kristineberg, Sweden. Odhner (1911*a*: 244).
—— [intestine] Plymouth, Devon, England. Nicoll (1914: 483).
—— [rectum] Whitstable, Kent, England. Maghraby & Perkins (1956: 486).
—— [?] East Frisian waters. Lammert (1974: 149).
Taurulus bubalus [?] Cullercoasts, Northumberland, England. Crofton (1947: 62).
—— [posterior intestine, rectum] Bergen, Norway. Køie (1976: 12).
Trachurus trachurus [?] Texel, Netherlands. Willemse (1968: 85).
Zeus faber [rectum] Plymouth, Devon, England. Nicoll (1914: 483).

Aspects of biology

Records of larval stages in the NE Atlantic:

(i) First intermediate host

Buccinum undatum [? 'the young distomes appear abundantly without tails in the sporocyst ... in the *Buccinum undatum* of our coast'] – presumably Belgium. van Beneden (1876: 194, also 1875: 173 = *Z. viviparus* according to Køie, 1969: 261).
—— [?] Boulogne, France. Pelseneer (1906: 170 as *Cercaria giardi*).
—— ['digestive gland unhealthy pinkish yellow – cercariae in sporocysts occupying almost whole of spire of shell' sporocyst and cercaria 'almost certainly a larval stage of *Zoogonus viviparus*'.] presumably at Plymouth. Lebour (1918: 514).
—— [digestive gland, gonad] Øresund, Sweden. Køie (1968: 21; 1969: 261; 1971: 165; 1974: 417; 1976: 3).
—— [?] ?Scotland. McNair, in DAFS (1972: 34).
—— [?] Heligoland. Lauckner (1973: 73; 1980: 374).

(ii) Second intermediate hosts

(a) Echinoderms

Leptosynapta inhaerens [peribuccal tentacles] Roscoff, Finistère, France. Cuénot (1892: 9 as *Cercaria capriciosa*).
Ophiothrix fragilis [gonads, viscera] Roscoff, Finistère, France. Cuénot (1892: 9 as *Cercaria capriciosa*).
Ophiura albida [gonads, viscera] Roscoff, Finistère, France. Cuénot (1892: 9 as *Cercaria capriciosa*).
—— ['everywhere'] Øresund, Sweden. Køie (1976: 6 – most highly infested natural second intermediate host, also has been experimentally infested),
Ophiura robusta [?] Øresund, Sweden. Køie (1976: 6 – one in 1 of 50 in area where *O. albida* is rarely infested).
Ophiura texturata [?] Øresund, Sweden. Køie (1976: 6 – naturally 1 in 1 of 20, also experimentally).

(b) Polychaetes

Ammotrypane aulogaster [?] West Kattegat. Køie (1976: 7 – once).
Amphicteis gunneri [?] West Kattegat. Køie (1976: 7 – once).
Gattyana cirrosa [?] West Kattegat. Køie (1976: 7 – once).
Lagis koreni [?] Øresund, Sweden. Køie (1976: 7 – naturally one or two in nearly half of 30, also experimentally).
Trochochaeta multisetosa [palps, anterior segments] Gullmar and Ellos Fjords, West Sweden. Orrhage (1973: 179).
various polychaetes [?] ? Scotland. McNair, in DAFS (1972: 34).

(c) Lamellibranch molluscs

(?) *Lima hians* [mantle edge] Millport, Firth of Clyde, Scotland. Nicoll & Small (1909: 241; as *Cercaria limae* – see Lauckner, 1983: 690).
(?) *Macoma baltica* [?] Burry Inlet, South Wales. James, Sannia & Bowers (1977: 13; as *Metacercaria limae* – see Lauckner, 1983: 690).
Nuculana minuta [?] Øresund, Sweden. Køie (1976: 7 – rarely, naturally and experimentally).
Nuculana pernula [mantle edge, occasionally in gills] Øresund, Sweden. Køie (1976: 7 – naturally and experimentally).

(d) Gastropod molluscs

Cythara attenuata [mantle] West Kattegat. Køie (1976: 7 – in 2 of 20).
Lora turricula [mantle] West Kattegat. Køie (1976: 7 – in 8 of 40).
Nassarius incrassatus [mantle] West Kattegat. Køie (1976: 7 – in 1 of 30).

(e) Crustaceans

(?) *Mysis* sp. [body-cavity] Roscoff, Finistère, France. Cuénot (1892: 9) believed that Villot's (1878: 30) record of *Cercaria megalocotylea* was possibly equivalent to his *Cercaria capriciosa*.

Lauckner (1973) and Køie (1976) also managed to infect a number of second intermediate hosts which were not found to harbour *Z. viviparus* naturally. Lauckner infected the echinoderm *Psammechinus miliaris*, while Køie infected the echinoderms *Ophiura affinis, Amphiura filiformis, A. chiajei, Ophiocomina nigra* and *P. miliaris*, the lamellibranchs *Nucula sulcata, Modiola marmorata, Spisula subtruncata, Corbula gibba, Venus striatula* and *V. ovata* and the gastropod *Aporrhais pespelicani*.

Køie (1980*a*) described the miracidium within the membranous non-operculate egg-capsule. The entire surface, apart from the apical papilla, is covered by a homogeneous layer of regularly arranged cilia. The next generation is found inside.

Mature daughter-sporocysts are found in the tissue between the tubules of the digestive gland, and released cercariae are most commonly found in this organ. The location of other cercariae suggests that it is possible that the cercariae leave the whelk through the mantle epithelium, distal to the kidney.

The tail-less cercaria, which bears a simple, pointed stylet, has been described by Lebour (1918) and Køie (1976). The ultrastructure and histochemistry were described by Køie (1971, 1974). On leaving the first intermediate host the cercariae creep, leech-like, using the posterior end and the oral sucker. The posterior end is distinctly sucker-like as can be seen in the scanning-electron-micrographs of Køie (1971, 1976). Under experimental conditions the cercariae were observed penetrating the polychaete *Lagis koreni* and, after bending ventrally, formed a thin, transparent spherical or oval cyst within less than an hour. The surface ultrastructure changes greatly in the first 40 days of the sojourn in the second intermediate host in that the microvilli atrophy and the spines become shorter, but the size of the worm does not alter during this period.

Cercaria zoogonoides Chubrik, 1966, from the gastropods *Sipho islandicus* and *Buccinum finmarchianum* from the Barents Sea could represent this species or possibly *Pseudozoogonoides subaequiporus*.

In general, the most important second intermediate hosts in the Øresund are ophiuroid echinoderms, particularly *Ophiura albida*, in which there is no apparent host-reaction to the parasite. Other echinoderms are only rarely infested. Køie (1976) suggested that polychaetes are probably important hosts only in regions where ophiuroids are rare, but it seems that many hosts of *Z. viviparus* apparently prey heavily on polychaetes and rarely pick up ophiuroids. Molluscs are generally poor hosts. The cercariae enter the ophiuroids mainly between the shields on the arms and encyst in all parts of the arms (as well as many other parts of the body) sometimes forming bulges. In the polychaete *L. koreni*, under experimental conditions, hundreds of cercariae were found, and heavily infested worms died within a day. Smaller infestations caused less damage, but sometimes granulomata were formed around the metacercariae. In the tubicolous polychaete *Trochochaeta multisetosa*, Orrhage (1973) found the metacercariae in the palps and anterior few segments only; this is the part of the body which is protruded from the tube and is therefore most liable to predation by fishes. In lamellibranchs (e.g. *Nuculana pernula*), although no host-reaction is evident, the metacercariae usually die and form hard, brown deposits.

Lauckner (1983) thought that 'in all probability, *C. [ercaria] limae* is the second larval stage of *Zoogonoides viviparus*'. This immature worm recorded in *Lima hians* from Millport, Scotland (Nicoll & Small, 1909) and *Macoma baltica* from Burry Inlet, South Wales by James *et al.* (1977), has been considered a fellodistomid metacercaria by Nicoll & Small (1909) and Bray & Gibson (1980). The tegument lacks spines but the short saccular excretory vesicle, and the position of the cyst attached to the inner edge of the mantle cavity, suggest that Lauckner may be correct.

The adult normally occurs in the posterior intestine, and, particularly, the rectum of various teleosts (see fig. 14 of MacKenzie & Gibson, 1970), lying deep between the irregular corrugations and adhering strongly with the ventral sucker. In the flounder *(Platichthys flesus)* they often lie close to the rectal valve which may serve to protect the worms from abrasion by gut-contents such as mollusc and echinoderm remains. In *in vitro* experiments Gibson (1971) found that *Z. viviparus*

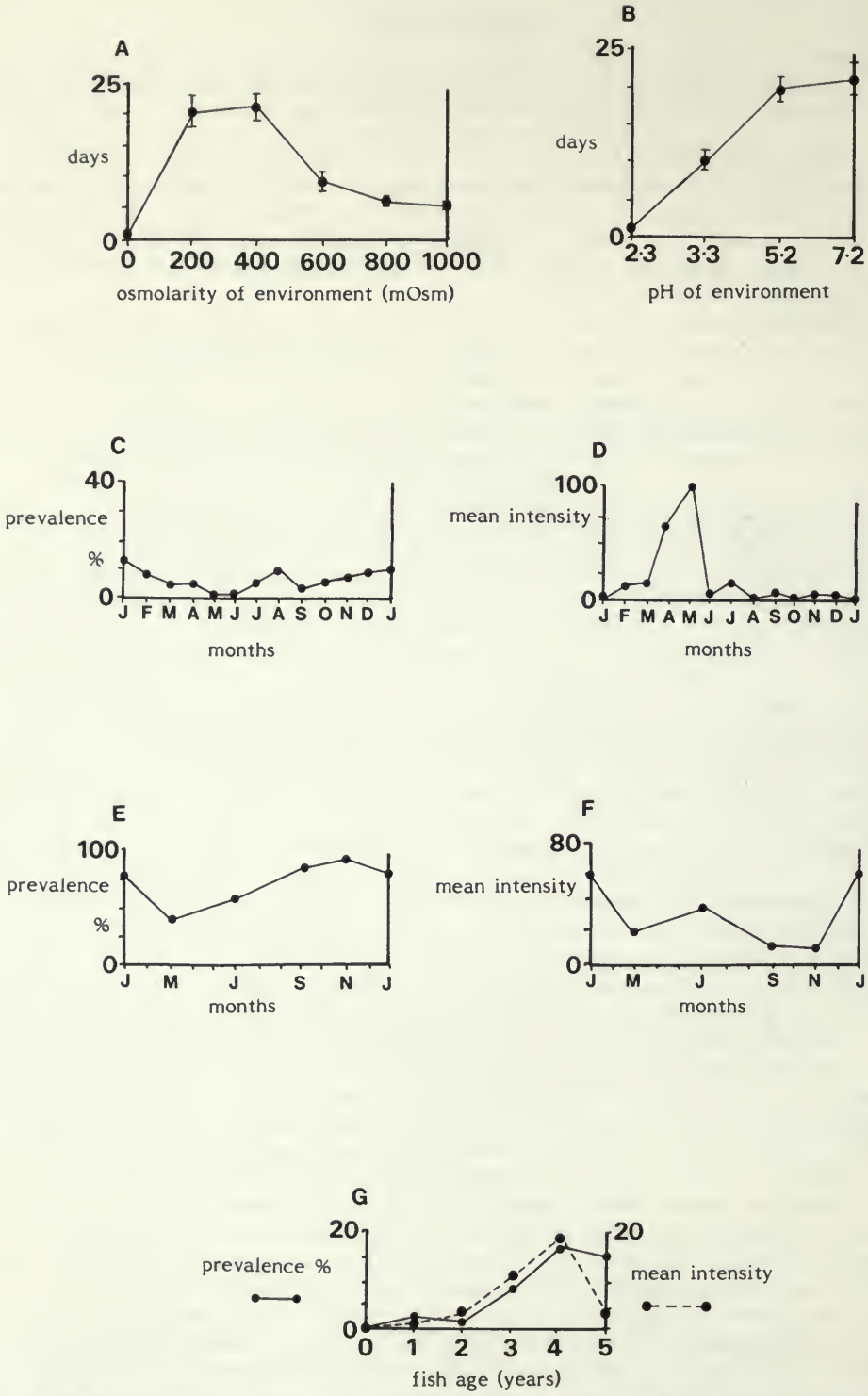


Fig. 9 Studies on *Zoogonoides viviparus* (Olsson) from *Platichthys flesus*, Scotland. (A) Osmolarity and survival *in vitro*; (B) pH and survival *in vitro*. (Error bars indicate twice the standard error of the mean survival); (C) Seasonal prevalence, Ythan estuary; (D) Seasonal mean intensity, Ythan estuary; (E) Seasonal prevalence, sea off Aberdeen; (F) Seasonal mean intensity, sea off Aberdeen; (G) Host-age and prevalence and mean intensity, Ythan estuary (After Gibson, 1971.)

survives most successfully in osmolarities of between 200 and 400 mOsm (Fig. 9A) and at a high pH (Fig. 9B), conditions which correspond to those found in the flounder rectum (Mackenzie & Gibson, 1970). It is commonly found in flatfish, and a number of other teleosts, notably *Callionymus* (Callionymidae/Gobiesociformes), *Zeus* (Zeidae/Zeiformes), sculpins (Cottidae/Scorpaeniformes), blennies (Blenniidae) and gobies (Gobiidae – both Perciformes). It appears that *Callionymus* spp. are among the preferred hosts. Frequently the rectum and the posterior third of the intestine of *C. lyra* is 'carpeted' with numerous (up to 800) specimens of *Z. viviparus*. We have found up to 416 in the flounder in the sea off Aberdeen, and in Danish waters nearly 100 % of the *Limanda limanda* specimens are infested, with up to 200 per host (Køie, 1983). Its distribution includes the north Atlantic, Mediterranean, Barents and White Seas and the northern Pacific Ocean. It is recorded from *Hippoglossoides platessoides* in the north-west Atlantic by Scott (1973, 1975*a,b*), Umnova (1979) and Zubchenko (1980), but all our zoogonine specimens from this host in that area belong to *Pseudozoogonoides subaequiporus* (see Bray, 1979; as *Diphterostomum microacetabulum*) and Scott (1982) reidentified his material as *D. microacetabulum*. Some of the records from the Pacific Ocean may be questionable, e.g. Shimazu (1974) questioned the record of Isakova-Keo (1952), who recorded *Z. viviparus* from the cyprinid *Leuciscus brandti*, believing these specimens to be close to his species *Pseudozoogonoides ugui*. The other two descriptions of the north Pacific form, those of Zhukov (1960) and Ichihara *et al.* (1966), also suggest that a different species may be involved in the northern Pacific records, e.g. both descriptions show that the caeca pass the testes, and the testes are well forward. Køie (1983) pointed out that *Buccinum undatum* does not occur in the North Pacific. Thus it may be that the northern Pacific form is different to that of the north Atlantic and should be carefully compared with *Zoogonoides acanthogobii* Yamaguti, 1938 and *Z. yamagutii* Kamegai, 1973.

Gibson (1972) showed that *Z. viviparus* has a higher prevalence in marine than in estuarine flounders, and was able to utilize this species as an indicator (tag) of the area of origin of the flounders. It has 'very high' prevalence in the sea off Aberdeen but 'very low' prevalence in the estuary he investigated in detail, the Ythan at Newburgh, Grampian region of Scotland. Results for these localities, along with three others (Gibson, 1971) are given in Table 7. In contrast to those in the sea, the estuarine flounders show low levels of prevalence and intensity throughout the year (Fig. 9C,D) (although one or two fishes of marine origin probably exert an influence on March to May figures in Fig. 9D). The results from marine flounders (Fig. 9E,F) suggest that their main period of parasite acquisition is in the autumn, and as the estuarine flounders pass into the sea in spring to spawn, they are not exposed to the peak period of parasite acquisition and, although most of their *Z. viviparus* burden is acquired at this time they never have the opportunity to build up higher intensity levels. The presence of estuarine flounders in the sea in spring probably influences the spring data (Fig. 9E) accounting partly for the spring drop. The reasons for the low prevalence in the estuary may well be connected with the rarity of *Buccinum undatum*. Ophiuroids were not found in the diet of the Ythan estuary flounders. Køie (1983) found that the dabs from Køge Bay,

Table 7 *Zoogonoides viviparus* in *Platichthys flesus*

Locality	No. of fish examined	No. infested	Percentage prevalence	No. of parasites	Mean intensity
Ythan estuary	740	45	6	598	13·3
Sea off Aberdeen	170	116	68	3622	31·2
River Dee	50	8	16	494*	61·7*
Plymouth	42	18	43	464	25·8
Loch Ewe	7	6	86	52	8·7

*As pointed out by Gibson (1972), this figure is distorted by the presence in the Dee estuary of a marine flounder containing 361 specimens.

at the Baltic end of the Øresund, were not infested with *Z. viviparus* whereas at all her other, more marine, stations there was a high prevalence. Køie (1969) showed that the infestation of *B. undatum* in the Øresund is lowest in December and rises in spring, and Gibson's (1971) data agree with this, in that presumably the cercarial production builds up during spring and summer, and the metacercarial population builds up during summer and autumn. Host-age effects (Fig. 9G) suggest that the parasite intensity increases after the flounder has fed on copepods and while it is of the size to feed on annelids, but decreases when the flounder diet changes to include more molluscs and small fish.

PREVIOUS DESCRIPTIONS. Olsson (1868: 28); Odhner (1902: 62; 1911*a*: 243); Nicoll (1907: 83; 1909*a*: 16); Lebour (1908: 53); Johnstone (1909: 191); Køie (1976: 11); [Zhukov (1960: 29); Ichihara *et al.* (1966: 4)].

DESCRIPTION (Figs 3d, 10). Over 200 specimens were studied (including two in serial sections). The measurements are given in Table 8. Unflattened, the worms are fusiform (Fig. 10A,B): flattening of these very small trematodes, although sometimes useful for particular purposes, distorts the overall morphology. The tegument bears small spines in transverse rows in the forebody, down to about the level of the ventral sucker. The *oral sucker* is subterminal, globular and leads into a short prepharynx and thence to a small globular to oval *pharynx*. The distinct oesphagus is straight or slightly sinuous. It bifurcates just inside the posterior half of the forebody. The caecal length varies, reaching to a level just anterior to the testes and the posterior edge of the ventral sucker or just overlapping the testes either slightly or considerably, up to the posterior edge of the testes or just

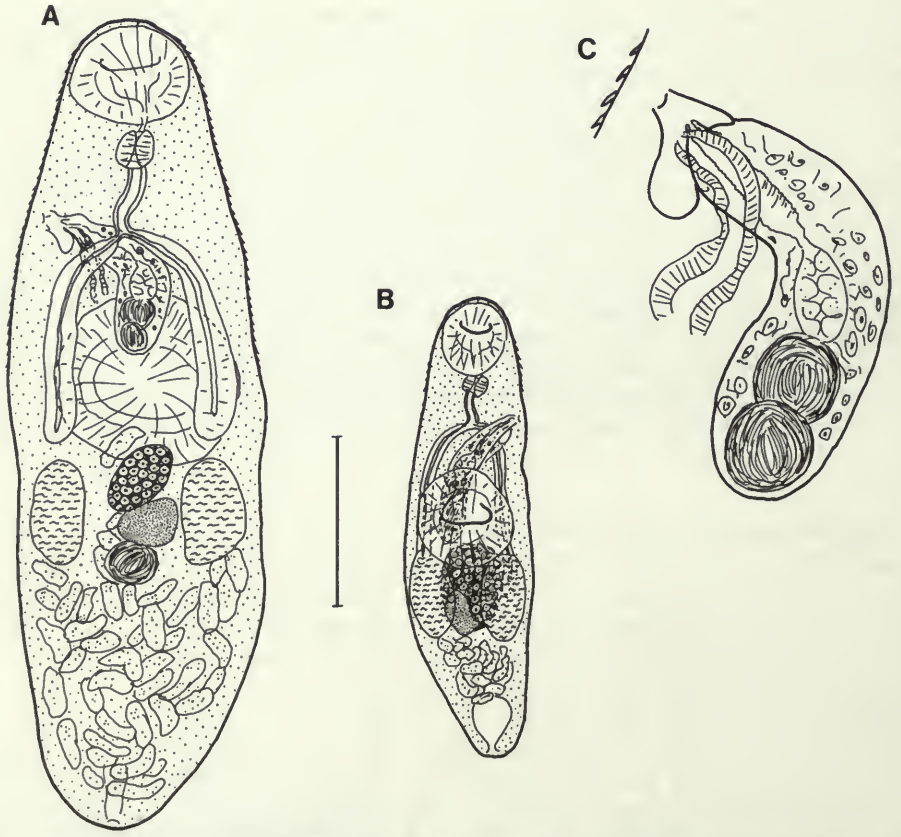


Fig. 10 *Zoogonoides viviparus* (Olsson). (A) Dorsal view, ex *Callionymus lyra*; (B) Ventral view, ex *Pomatoschistus minutus*; (C) Terminal genitalia. Scale bars: A, B 0·2 mm.

Table 8 Measurements of *Zoogonoides viviparus*

Host	*Callionymus lyra*	*Zeus faber*	*Pomatoschistus minutus*	Flatfish
Length (mm)	0·69–1·46	0·42–0·90	0·40–0·54	0·31–0·93
Breadth (mm)	0·24–0·34	0·18–0·28	0·10–0·15	0·13–0·34
Length : forebody ratio	1 : 0·30–0·42	1 : 0·33–0·40	1 : 0·27–0·37	1 : 0·26–0·50
Oral sucker (mm)	0·12–0·14 × 0·11–0·14	0·12–0·13 × 0·11	0·07–0·09 × 0·08	0·07–0·13 × 0·07–0·14
Ventral sucker (mm)	0·17–0·22 × 0·15–0·22	0·19 × 0·16–0·17	0·12–0·14 × 0·09–0·11	0·11–0·27 × 0·10–0·22
Sucker-ratio	1 : 1·36–1·60	1 : 1·45–1·54	1 : 1·125–1·37	1 : 1·10–2·00
Pharynx (mm)	0·04–0·06 diam.	0·04–0·05 diam.	0·03–0·04 diam.	0·03–0·06 diam.
Oesophagus (mm)	0·05–0·08	0·06	0·04	0·02–0·10
Cirrus-sac (mm)	straight 0·18–0·24 recurved* (A) 0·14–0·17 (B) 0·11–0·14 × 0·04–0·07	–	straight 0·15 recurved* (A) 0·11 (B) 0·10 × 0·03–0·04	straight 0·14–0·21 recurved* (A) 0·09–0·18 (B) 0·07–0·15 × 0·03–0·06
Testes (mm)	0·10–0·15 × 0·06–0·11	0·10–0·11 × 0·07	0·09–0·11 × 0·04–0·05	0·05–0·13 × 0·03–0·08
Ovary (mm)	0·05–0·12 × 0·05–0·09	0·08 × 0·07	0·09–0·10 × 0·06–0·08	0·05–0·10 × 0·04–0·08
Miracidium (μm)	60–70 × 25–36	62 × 25	52 × 20	45–82 × 17–62

*Recurved cirrus-sac length measured in two parts: (A) distal part, (B) proximal part.

beyond. The *ventral sucker* is larger that the oral sucker in the ratio 1 : 1·1–2·0. It lies just anterior to the middle of the body. It is strongly muscular and not quite circular, with a transversely oval aperture.

The terminal *excretory pore* leads via a narrow duct into a small, oval vesicle which just overlaps the uterus.

The oval *testes* lie symmetrically to slightly obliquely just posterior to or at the posterior margin of the ventral sucker with their long axes lying longitudinally. The vasa efferentia were not traced. The *cirrus-sac* is claviform and variable in that it may lie straight or be strongly or weakly reflexed, normally overlapping the ventral sucker almost to its middle. It contains a small, bipartite seminal vesicle, a short, wide, oval, vesicular pars prostatica and a long, muscular, wide, annularly wrinkled ejaculatory duct – all surrounded by numerous gland cells (Fig. 10C). Often the lining of the ejaculatory duct has been described as spined. Close examination of sections under oil immersion does not clearly show whether tiny spines are present or whether small papillae of the ejaculatory duct lining extend into the lumen. It is possible that the spine-like effect is the result of the wrinkling in the ejaculatory duct which occurs when it is withdrawn. If the cirrus-sac is reflexed the bend occurs at about the junction of the pars prostatica and ejaculatory duct or further posteriorly. It opens into a distinct genital atrium, which in turn opens via the genital pore close to or on the left lateral margin about half-way between the suckers. There is a distinct sac-like diverticulum (atrial sac) leading posteriorly from the genital atrium (Fig. 3D). The function of this is not obvious, but a similar structure is referred to as an 'accessory seminal receptacle' by Arai (1954).

The oval *ovary* is usually just smaller than the testes, just overlapping the posterior margin of the ventral sucker and between the testes. The long axis tends to lie diagonally. The oviduct passes posteriorly and receives the ducts of the seminal receptacle and the vitellarium. No Mehlis' gland

a
b
c
d
e
f
g
h
i

was detected. The canalicular seminal receptacle is globular. Laurer's canal apparently arises at or near the proximal end of the seminal receptacle and passes posteriorly opening dorsally, posteriorly to the seminal receptacle. The bulk of the hindbody is filled with the *uterus* containing the developing miracidia each enclosed in a thin membranous capsule. No shell is developed. The metraterm is strongly muscular and is ensheathed with gland cells distally. It opens into the genital atrium dorsally to the cirrus-sac. Between the seminal receptacle and the ovary lies the subglobular, oval or slightly irregular single *vitelline mass*.

DISCUSSION. Of the species mentioned in the synonymy, *Distoma callionymi* and *Cercaria megalocotylea* are too poorly known to be definitely considered synonyms, but in the former case the host suggests that the synonymy is likely. The status of this species is fairly straightforward, but the possibility of its confusion with *Pseudozoogonoides subaequiporus* (see pp. 147, 157) should be stressed

Subfamily **LEPIDOPHYLLINAE** Stossich, 1903

Key to the genera of the Lepidophyllinae from the north-east Atlantic

1 Body flattened, spatulate. Testes deeply lobed. Excretory pore subterminal. In urinary bladder . ***Lepidophyllum*** Odhner, 1902 (p. 160)

— Body more or less oval or rounded in cross-section. Oval to pyriform or fusiform in ventral view. Testes more or less entire. Excretory pore terminal. Not usually found in urinary bladder . . 2

2 Caeca short, saccular or not, reaching into hindbody 3

— Caeca reaching to testes or beyond 4

3 Testes overlapping ventral sucker into forebody. Ovary post-testcular. Vitellarium in forebody . ***Panopula*** Overstreet & Pritchard, 1977 (p. 171)

— Testes not reaching into forebody. Ovary pre-testicular. Vitellarium at or near level of ventral sucker of posterior forebody . . . . . ***Brachyenteron*** Manter, 1934 (p. 175)

4 Ventral sucker divided equatorially by ridge or row of large papillae 5

— Ventral sucker undivided . . . . . ***Steganoderma*** Stafford, 1904 (p. 193)

5 Ventral sucker divided equatorially by internal (ventral) ridge and external (dorsal) cleft . . . 6

— Row of large papillae across internal equator of ventral sucker. No dorsal cleft . . . . . ***Steganodermatoides*** Parukhin & Lyadov, 1979 (p. 181)

6 Genital atrium large, pocketed. Periatrial gland undivided, massive, also enveloping distal regions of metraterm and cirrus-sac . . . . . ***Neosteganoderma*** Byrd, 1964 (p. 185)

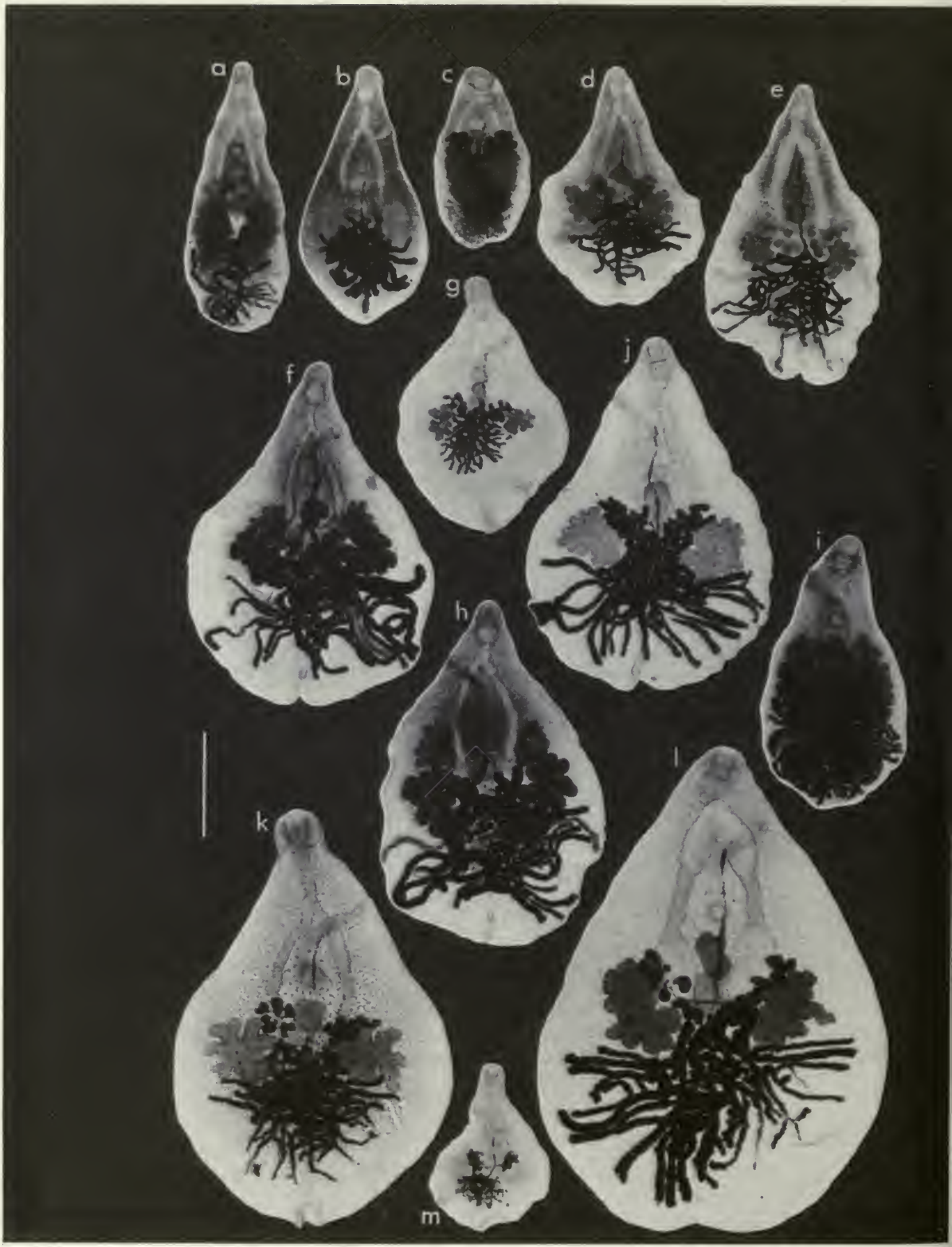
— Genital atrium small, tubular. Periatrial gland divided into separate, claviform sacs . . . . . ***Proctophantastes*** Odhner, 1911 (p. 189)

Genus ***LEPIDOPHYLLUM*** Odhner, 1902

Paralepidophyllum Yamaguti, 1934.

DIAGNOSTIC FEATURES. Body broadly pyriform; strongly flattened dorso-ventrally. Body surface spinous. Oral sucker small. Oesophagus distinct. Caeca reach into hindbody to level of vitellaria or testes. Ventral sucker small, rounded, in anterior half of body. Symmetrical lobed testes in mid to anterior hindbody. Cirrus-sac narrow, elongate. Seminal vesicle bipartite. Pars prostatica long. Genital pore sinistral, dorsally submarginal or marginal; mid to anterior forebody. Ovary oval to slightly lobed, in anterior hindbody. Eggs tanned, operculate. Filaments of egg-shell material may occur in uterus. Uterus mainly post-testicular. Vitellarium two groups each of about 9–13 follicles, laterally in anterior hindbody. Excretory pore dorsally subterminal, vesicle elongate sac in posterior hindbody. In urinary bladder of teleosts.

Fig. 11 (*left*). *Lepidophyllum steenstrupi* Odhner. Photomicrographs of specimens showing variation, all to same scale. ex *Anarhichas lupus:* (a) NE Scotland; (b) Faeroes; (c) Tromsø; (e) Nova Scotia; (g) Newfoundland: (h) Anton Dohrn Bank; (i) Passamaquoddy Bay. ex *Anarhichas minor*; (d) Iceland-Faroes Channel; (f) Anton Dohrn Bank. Scale bar: 1 mm.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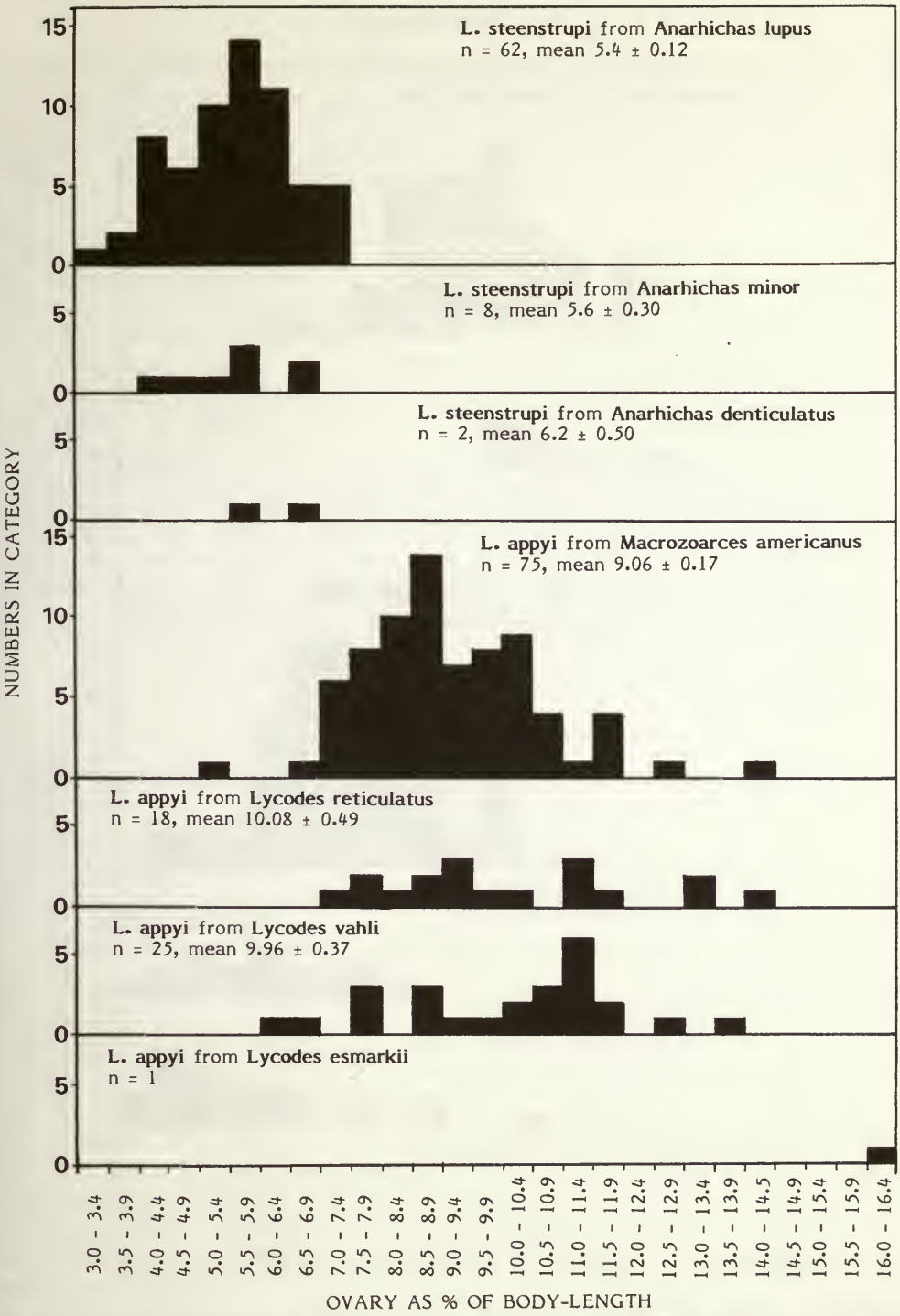

Fig. 13 *Lepidophyllum steenstrupi* and *L. appyi*, the length of the ovary as a percentage of body-length.

Fig. 12 (*left*). *Lepidophyllum appyi* sp. nov. Photomicrographs of specimens to show variation, all to same scale. ex *Lycodes vahli:* (a), (f), (h), (i) Newfoundland; (m) Gulf of St Lawrence. ex *Macrozoarces americanus:* (b), (k) Passamaquoddy Bay; (g) Gulf of St Lawrence. ex *Lycodes esmarkii:* (c) NW Scotland. ex *Lycodes reticulatus:* (d) Newfoundland; (e), (j), (l) Scotian Shelf. Scale bar: 1 mm.

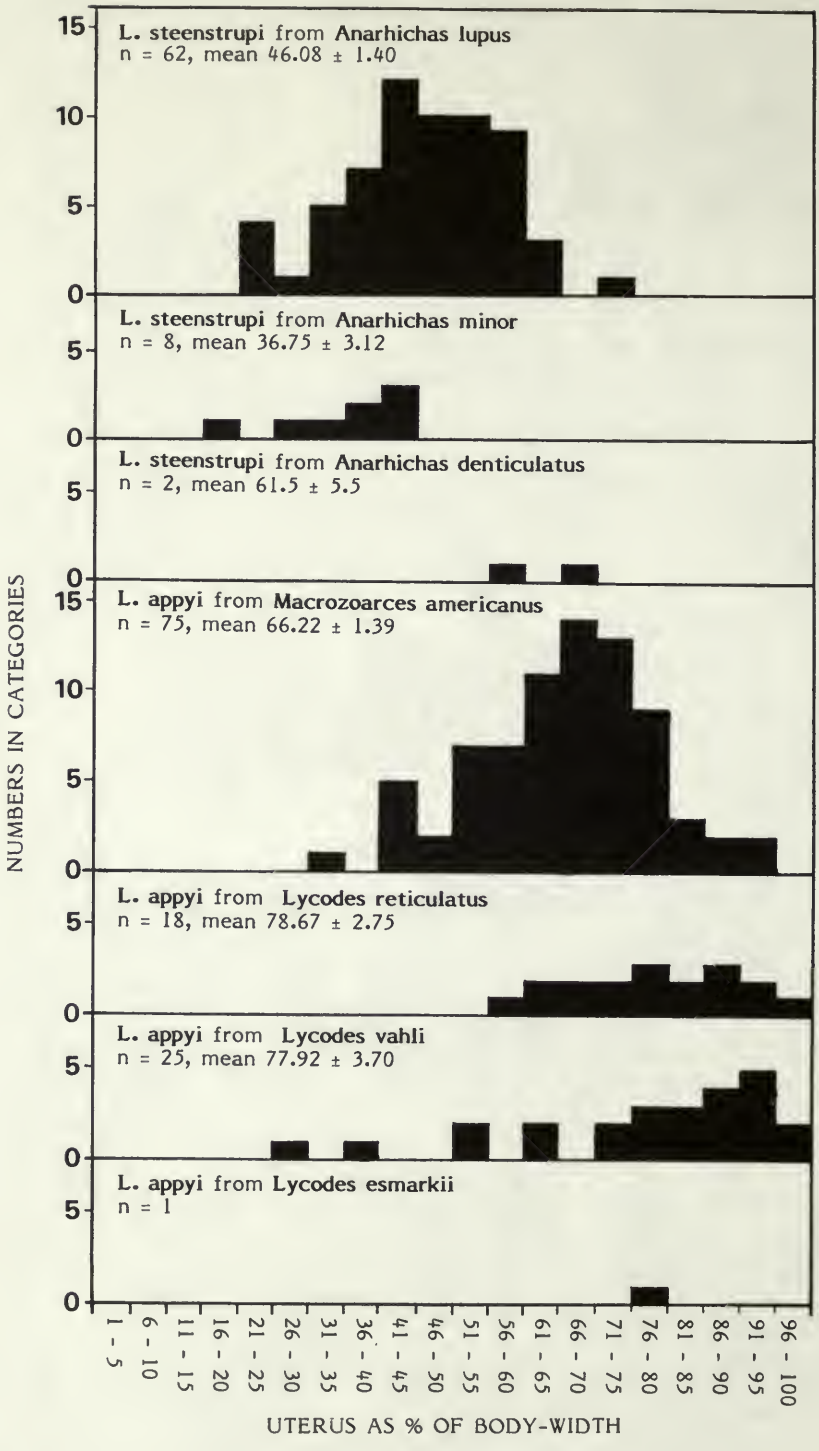

Fig. 14 *Lepidophyllum steenstrupi* and *L. appyi*, the uterus as a percentage of body-width.

COMMENTS. Two species are recognized in the north-east Atlantic which can be differentiated thus:

(a) Uterus always surrounded by wide band of parenchyma – no uterine slings reaching to body margin. Ovary always posterior to ventral sucker with distinct gap; oval to smoothly rounded; length 3–7 % of body length. Testes relatively smaller, less deeply lobed with fewer (average 5·6) lobes. Spines distinct but relatively small. In *Anarhichas* spp . . . . . *L. steenstrupi* Odhner, 1902 (p. 165)

(b) Uterus fills post-testicular region, or single slings tend to reach body-margin. Ovary often overlaps ventral sucker, close to or contiguous with ventral sucker; often smooth but may be distinctly but weakly lobed, length 7–14 % of body length. Testes relatively larger with more (average 7·7) lobes. Spines larger. In zoarcid teleosts . . . . . *L. appyi* sp. nov. (p. 168)

Both species, in particular *L. appyi,* are very variable and a series of microphotographs of each is included to illustrate this (Figs 11, 12). Conjectures on whether these forms are host-induced varieties (Bray, 1979) are rather premature. It seems most useful to erect a new species, in so doing drawing attention to the fact that there are two forms to be found in the north Atlantic, apparently strictly separated by host. The difference in ovary : body-length ratio, illustrated on Fig. 13 shows that there is little overlap in this feature. Fig. 14 showing the width of the extreme extent of the uterus as a percentage of the body-width indicates a difference which is much less distinct, but serves as a crude measure of the first point made in the key above. This feature is, unfortunately, not invariable (see Fig. 12) so that these two species must be considered to be separated by a polythetic assemblage of characters. The testicular lobation is statistically different using a simple statistical test (d-statistic – see Parker, 1973).

Lepidophyllum steenstrupi Odhner, 1902

TYPE-HOST AND LOCALITY. *Anarhichas minor,* Iceland.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Anarhichas lupus [urinary bladder] east coast of Iceland (66°N, 13°W; depth 119 m; Aug., 1948). (see Rees, 1953: 21). BM(NH) 1976.4.9.17.

—— [——] Eldey Bank, off Reykjanes, Iceland (64°N, 24°W; depth 148–152 m; May, 1974). BM(NH) 1982.10.8.1.

—— [——] Anton Dohrn Bank (65°N, 30°W; depth 370–440 m; May, 1974). BM(NH) 1982.10.8.2–6.

—— [——] Orkneys (59°N, 04°W; depth 164–172 m; July, 1976). BM(NH) 1982.10.8.7.

—— [——] Faeroes (62°N, 08°W; depth 112 m; July, 1976). BM(NH) 1982.10.8.9.

—— [——] Moray Firth (58°N, 02°W; depth 150–152 m; July, 1976). BM(NH) 1982.10.8.8.

—— [——] NE Scotland (59°N, 01°E; depth 107–117 m; Dec., 1979). BM(NH) 1982.10.8.10–13.

—— [——] Tromsø, Norway (June, 1980). BM(NH) 1982.10.8.14.

—— [——] Bell Rock, North Sea (56°N, 02°W; depth 52 m; May, 1982); Swatchway, North Sea (57°N, 00°; depth 80 m; June, 1982); Beryl, North Sea (60°N, 02°E; depth 118 m; June, 1982); NW of Ninian Field, North Sea (61°N, 01°E; depth 150 m; May, 1983); SW of Ninian Field, North Sea (61°N, 01°E; depth 140 m; May, 1983); West of Bressay Bank, North Sea (59°N, 00°; depth 140 m; June, 1983); Strathey Point, N. of Scotland (59°N, 04°W; depth 100 m; June, 1983). BM(NH) 1983.11.23.16.

Anarhichas minor [urinary bladder] Anton Dohrn Bank (65°N, 30°W; depth 370–440 m; May, 1974). BM(NH) 1982.10.8.15.

—— [——] Iceland–Faeroes Channel (63°N, 11°W; depth 410–420 m; June, 1974). BM(NH) 1982.10.8.16.

(b) From elsewhere

Anarhichas denticulatus [urinary bladder] Newfoundland. Material of Bray (1979: 418). BM(NH) 1977.2.15.139.

Anarhichas lupus [urinary bladder] Newfoundland and Nova Scotia. Material of Bray (1979: 418). BM(NH) 1977.2.15.112–138.

—— [——] Passamaquoddy Bay, New Brunswick (May, 1976). Collector R. Appy. BM(NH) 1983.3.16.27.

(ii) NE Atlantic records from the literature
Anarhichas lupus [urinary bladder] Trondheim, Norway. Odhner (1911*a*: 240).
—— [——] Kristineberg, Sweden. Odhner (1911*a*: 240).
—— [——] east coast of Iceland. Rees (1953: 21).
—— [——, gall-bladder] Neskaupstadur and Húsavík, Iceland. Brinkmann (1956: 15).
Anarhichas minor [urinary bladder] Iceland. Odhner (1902: 68: 1911*a*: 240).
—— [——] Neskaupstadur and Húsavík, Iceland. Brinkmann (1956: 15).

ASPECTS OF BIOLOGY. Little is known of the life-cycle of this species. It develops from a narrow lanceolate form (Figs 12a,f, 15B) to a wide, spatulate form (Figs 12b,g, 15A) while within the urinary bladder (see also Brinkmann, 1975). The route of entry to the urinary bladder is not known. Specimens have not been detected in the intestine or the ureter, but the opening of the urinary bladder is distinct from the anus so the latter seems the more likely point of entry. A record of a single specimen in the gall-bladder is given by Brinkmann (1956). This worm is known exclusively from *Anarhichas* spp.; records from *Macrozoarces americanus* (see Stafford, 1904; 1907; Cooper, 1915: Linkletter *et al.*, 1977) and *Lycodes* spp. (see Bray, 1979) are considered to represent a separate but closely related species, *L. appyi*. *L. steenstrupi* is restricted to the North Atlantic Ocean and the Barents and White Seas.

PREVIOUS DESCRIPTIONS. Odhner (1902: 68; 1911*a*: 240); Stafford (1904: 487); Miller (1941: 47); Rees (1953: 21); Brinkmann (1975: 43).

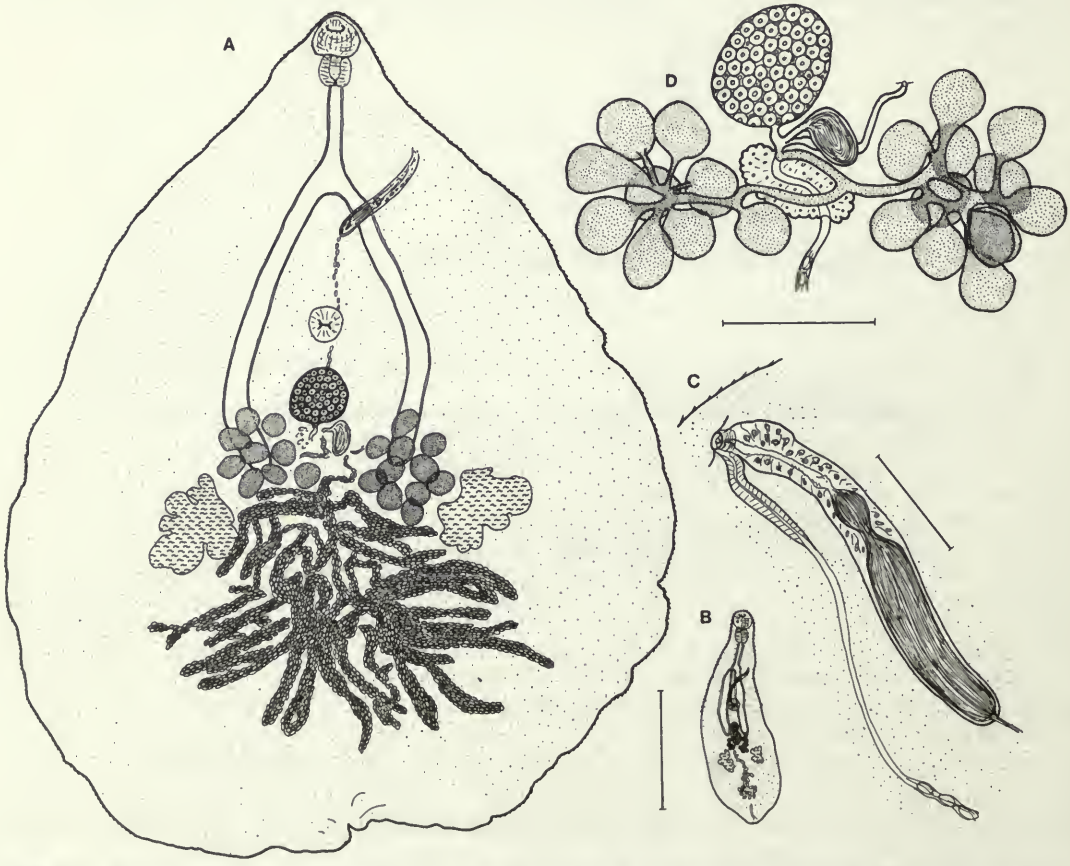

Fig. 15 *Lepidophyllum steenstrupi* Odhner. (A) Ventral view, ex *Anarhichas lupus*; (B) Ventral view, ex *A. minor*; (C) Terminal genitalia; (D) Proximal female genitalia. Scale bars: A, B 1 mm, C 0·2 mm. D. 0·5 mm.

Table 9 Measurements of *Lepidophyllum steenstrupi*

Authority	Odhner (1902)	Present study		
Host	*Anarhichas minor*	*Anarhichas lupus*	*Anarhichas minor*	*Anarhichas denticulatus*
Locality	Iceland	see text	see text	see text
Number studied	–	62	8	2
Length (mm)	2·1–2·4	0·92–5·45	1·45–3·1	3·85–4·68
Breadth (mm)	1·1–1·4	0·49–3·3	0·47–1·83	1·9–2·1
Length : forebody ratio	[1 : 0·34]*	1 : 0·31–0·40	1 : 0·37–0·46	1 : 0·32
Oral sucker (mm)	*c.* 0·18 diam.	0·11–0·24 × 0·12–0·28	0·11–0·17 × 0·12–0·18	0·21–0·22 × 0·23–0·24
Ventral sucker (mm)	*c.* 0·17 diam.	0·09–0·19 × 0·09–0·20	0·11–0·17 × 0·10–0·17	0·20–0·23 × 0·20–0·23
Sucker-ratio	[*c.* 1 : 0·94]	1 : 0·58–0·95	1 : 0·83–1·00	1 : 0·87–0·96
Pharynx (mm)	0·12 × 0·13	0·09–0·20 × 0·08–0·22	0·09–0·14 × 0·08–0·13	0·16–0·18 × 0·18–0·20
Oesophagus (mm)	–	0·05–0·45	0·13–0·37	0·33–0·42
Cirrus-sac (mm)	–	0·41–0·75 × 0·03–0·08	0·23–0·56 × 0·03–0·05	0·55–0·59 × 0·07
Testes (mm)	–	0·27–0·73 × 0·13–0·46	0·12–0·55 × 0·10–0·34	0·61–0·72 × 0·32–0·50
Testes lobation	[*c.* 3]	2–9 [av. 5·44]	4–9 [av. 5·93]	6–8 [av. 6·75]
Ovary (mm)	–	0·10–0·31 × 0·07–0·40	0·07–0·18 × 0·07–0·22	0·26–0·28 × 0·23–0·24
Body-length : ovary ratio	[1 : 0·07]	1 : 0·04–0·07	1 : 0·04–0·07	1 : 0·06–0·07
Vitelline follicles				
poral	[10]	9–12 [av. 11·5]	8–12 [av. 10·3]	12
aporal	[8]	9	8–10 [av. 8·67]	9
Eggs (μm)	43 × 21	35–43 × 18–20	37–42 × 17–20	35–42 × 15–21

*Square brackets—measurements taken from published figure.

DESCRIPTION (Figs 11, 13, 14, 15). This description is based on many specimens, the measurements, meristic features and numbers of specimens are given in Table 9. The worms are flattened, with a fusiform to broadly pyriform outline (Figs 11, 15A,B). Much of the surface of the worm has irregularly spaced peg-like or scale-like spines. At the posterior end they are embedded in the tegument. The *oral sucker* is subglobular with a terminal opening. A minute prepharynx leads to a large, subglobular *pharynx* and a distinct oesophagus. The intestinal bifurcation is in about the middle of the forebody. The caeca, which may be narrow or wide, reach just posterior to the ovary. In larger specimens they may terminate at the level of the testes, but generally they terminate just anteriorly to the testes, usually in the vitelline field or, occasionally, median to it. The circular ventral sucker protrudes slightly from the surface of the worm and is normally slightly larger than the oral sucker.

The *excretory pore* lies just dorso-subterminally, just anterior to a slight notch in the middle of the posterior margin of the worm. The vesicle is an elongate sac, reaching forward for about a quarter of the length of the hindbody. It is fed by a complex system of small convoluted tubules.

The large *testes* lie laterally, subsymmetrically in the anterior half of the hindbody. They are distinctly lobate. The vasa efferentia pass from the anterior part of the median edge of the testes and pass diagonally forward, apparently uniting just posteriorly to the cirrus-sac to form a short

vas deferens, which in turn passes through the posterior extremity of the cirrus-sac, swelling there to form a bipartite seminal vesicle, whose posterior part is much the larger. This posterior moiety is an elongate sac, the anterior part is an oval chamber. The pars prostatica is long, with a narrow lumen, and changes imperceptibly to form a fairly weakly muscular ejaculatory duct. The *cirrus-sac* is narrow and elongate–oval, having parallel sides for much of its length (Fig. 15C). It has a distinct, if not thick, muscular wall. It may reach, or just overlap the ventral sucker, but, as the worm elongates, the forebody apparently lengthens more rapidly than the cirrus-sac and in the larger worms the cirrus-sac terminates well within the forebody (Fig. 15A). Its posterior end lies quite near to the dorsal surface, but the sac loops ventrally to the left caecum before opening into a small genital atrium, which opens sublaterally on the *dorsal* surface of the sinistral side of the mid-forebody, through a small eminence.

The small, subglobular *ovary* (Fig. 13) lies just posteriorly to, or just overlapping, the ventral sucker. A short oviduct passes posteriorly, receives the ducts from the canalicular seminal receptacle and Laurer's canal, more of less together, then receives the common vitelline duct before passing into Mehlis' gland. The seminal receptacle lies just posteriorly to the ovary and may be larger than the ovary, or much smaller. Laurer's canal is short and opens dorsally at about the level of the ovary. The *uterus* consists of a number of irregularly radiating slings, lying posteriorly to the gonads. There is always a large area of unoccupied parenchyma between the uterus and the body margin (Fig. 14). A single uterine sling, in which the eggs lie in a single file, passes anteriorly between the vitelline fields and enters the genital atrium via a strongly muscular metraterm. The uterus contains not only numerous small operculate eggs but also numerous narrow strands of egg-shell material. It is not clear whether these are egg-filaments or unattached strands. The vitelline duct passes posteriorly from the oviduct, bifurcates, and the two collecting ducts run laterally to a point at about the centre of the cluster of *vitelline follicles* (Fig. 15D). These follicles lie in two lateral fields between the testes and the ovary and are fairly uniformly subglobular and constant in number (Table 9).

Discussion. This is a distinct species, and the only controversy surrounding its taxonomy is its relationship to the *Lepidophyllum* from zoarcids in the north Atlantic which we have described as *L. appyi*. Odhner's original description is of a fairly young lanceolate worm, but subsequent authors (e.g. Miller, 1941; Brinkmann, 1975) have had no difficulty in recognizing their wide spatulate forms as being conspecific and representing different developmental phases.

Lepidophyllum appyi sp. nov.

Lepidophyllum steenstrupi Odhner, 1902 of Bray (1979) in part and probably Stafford (1904, 1907) in part, Linkletter *et al.* (1977) in part and Cooper (1915).

Type-host and locality. *Lycodes vahli,* Grand Banks, Newfoundland.

Records

(i) Material studied
(a) From the NE Atlantic
Lycodes esmarkii [urinary bladder] off NW Scotland. BM(NH) Paratype 1983.3.16.1.

(b) From elsewhere
Lycodes reticulatus [urinary bladder] Grand Banks, Newfoundland. Material of Bray (1979: 419; as *L. steenstrupi*). BM(NH) Paratypes 1977.2.15.140–155.
—— [——] Scotian Shelf (44°N, 63°W; and 42°N, 66°W; July, 1975). Collector: R. Appy. BM(NH) Paratypes 1983.3.16.2–4.
—— [——] Gulf of St Lawrence (62°N, 49°W; Sept., 1975). Collector: R. Appy. BM(NH) Paratypes 1983.3.16.5–6.
Lycodes vahli [urinary bladder] Sable Island Bank, Nova Scotia. Material of Bray (1979: 419; as *L. steenstrupi*) BM(NH) Paratypes 1977.2.15.157–185.
—— [——] Grand Banks, Newfoundland. Material of Bray (1979: 419; as *L. steenstrupi*). BM(NH) Holotype 1977.2.15.156. Paratypes 1977.2.15.157–185.

—— [——] Funk Island Bank, Newfoundland. Material of Bray (1979: 419; as *L. steenstrupi*). BM(NH) Paratypes 1977.2.15.157–185.
—— [——] Gulf of St Lawrence. (48°N, 63°W; May, 1975). Collector: R. Appy. BM(NH) Paratypes 1983.3.16.7–10.
Macrozoarces americanus [urinary bladder] Passamaquoddy Bay, New Brunswick (May, June, 1975; May, Nov., 1976). Collector: R. Appy. BM(NH) Paratypes 1983.3.16.11–19, also material lent by R. Appy; and (Aug., 1982). BM(NH) Paratypes 1983.3.16.20.
—— [——] Gulf of St Lawrence (48°N, 65°W; May, 1975; 48°N, 64°W, Sept., 1975). Collector: R. Appy. BM(NH) Paratypes 1983.3.16.21–25 also material lent by R. Appy.
—— [——] Scotian Shelf (45°N, 66°W; July, 1975). Collector: R. Appy. BM(NH) Paratypes 1983.3.16.26.

(ii) NE Atlantic records from the literature
None.

ASPECTS OF BIOLOGY. The four species of fish recorded as hosts are all members of the family Zoarcidae and the distribution covers the north-west and north-east Atlantic. As with *L. steenstrupi*, nothing is known of the life-cycle, transmission or route of invasion of this worm.

PREVIOUS DESCRIPTIONS. None.

DESCRIPTION (Figs 12, 13, 14, 16). This description is based on many specimens, the numbers of which are included with the measurements on Table 10. The worms are flattened, with a fusiform to spatulate outline (Figs 12, 16), and bear prominent tegumental spines, reaching well into the hindbody. The subglobular *oral sucker* opens subterminally to terminally and leads via a short prepharynx to a large, subglobular *pharynx* and a distinct oesophagus which bifurcates in about the middle of the forebody giving rise to caeca which reach into the hindbody and terminate in the vitelline field. The *ventral sucker* lies in the anterior half of the body and is generally distinctly smaller than the oral sucker.

The *excretory pore* is dorsally subterminal and leads to a short, narrow vesicle which reaches to the uterus.

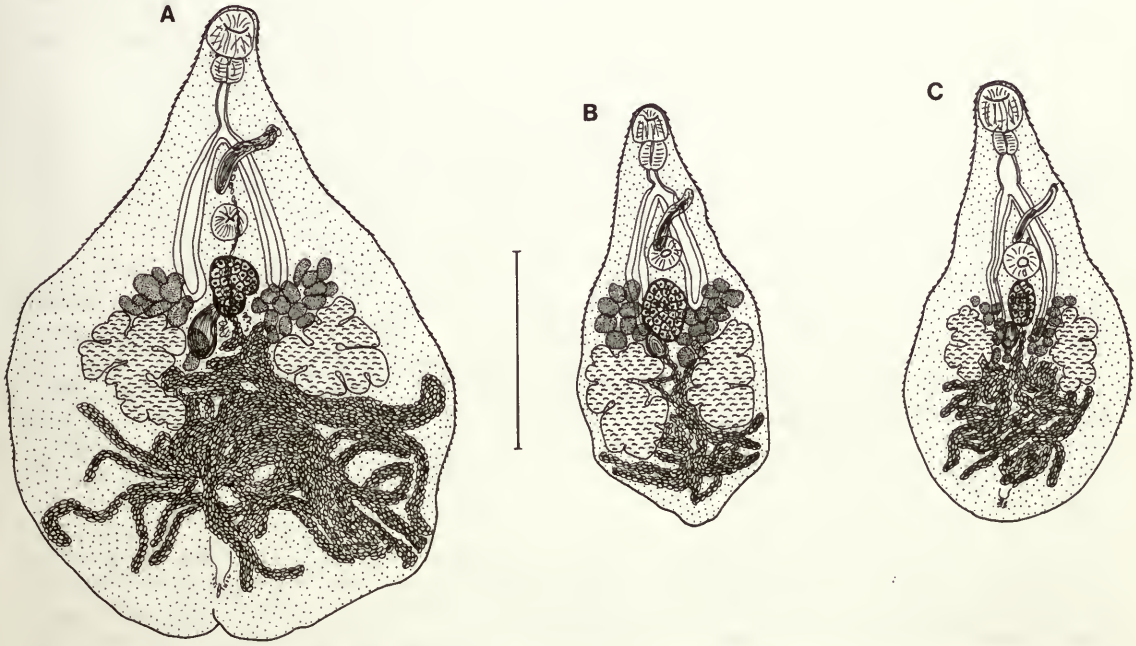

Fig. 16 *Lepidophyllum appyi* sp. nov. (A), (B) Ventral views, ex *Lycodes vahli*; (C) Ventral view, ex *Macrozoarces americanus*. Scale bar: 1 mm.

Table 10 Measurements of *Lepidophyllum appyi*

Host	*Lycodes vahli*	*Lycodes reticulatus*	*Lycodes esmarkii*	*Macrozoarces americanus*
Number studied	25	18	1	77
Length (mm)	1·45–3·54	2·17–4·60	1·75	1·80–4·18
Breadth (mm)	0·65–2·35	1·57–2·30	0·9	0·95–2·85
Length : forebody ratio	1 : 0·29–0·41	1 : 0·32–0·38	1 : 0·24	1 : 0·33–0·40
Oral sucker (mm)	0·13–0·26 × 0·13–0·27	0·18–0·24 × 0·18–0·22	0·22 × 0·25	0·20–0·39 × 0·21–0·41
Ventral sucker (mm)	0·12–0·22 × 0·11–0·22	0·15–0·22 × 0·15–0·21	0·21 × 0·23	0·18–0·29 × 0·17–0·31
Sucker-ratio	1 : 0·78–0·95	1 : 0·83–1·05	1 : 0·92	1 : 0·67–0·86
Pharynx (mm)	0·10–0·17 × 0·09–0·19	0·10–0·17 × 0·12–0·18	0·13 × 0·12	0·12–0·22 × 0·13–0·21
Oesophagus (mm)	0·12–0·32	0·15–0·30	0·05 (at least)	0·16–0·35
Cirrus-sac (mm)	0·20–0·45 × 0·03–0·09	0·30–0·63 × 0·04–0·10	0·37 × 0·06	0·33–0·90 × 0·06–0·13
Testes (mm)	0·16–0·66 × 0·19–0·57	0·35–0·63 × 0·32–0·65	0·40–0·56 × 0·25–0·42	0·36–0·73 × 0·20–0·70
Testes lobation	5–14 (av. 7·85)	5–11 (av. 7·3)	5–6	7–10 (av. 7·6)
Ovary (mm)	0·11–0·40 × 0·11–0·29	0·17–0·47 × 0·18–0·25	0·28 × 0·22	0·18–0·34 × 0·14–0·31
Body-length : ovary ratio	1 : 0·06–0·14	1 : 0·07–0·14	1 : 0·16	1 : 0·05–0·14
Vitelline follicles				
poral	10–18 (av. 11·95)	13–14 (av. 13·5)	10	10–12 (av. 10·87)
aporal	8–14 (av. 9·2)	10–12 (av. 10·5)	9	7–10 (av. 8·12)
Eggs (μm)	35–41 × 16–22	38–45 × 19–25	39–44 × 18–26	33–43 × 17–26

The deeply lobed, large *testes* lie symmetrically in the anterior to mid-hindbody. The long, narrow *cirrus-sac* contains a bipartite seminal vesicle, with the proximal part an elongate sac and the distal part a smaller globular sac, a short pars prostatica and ejaculatory duct. It opens, via the genital atrium, on the submarginal dorsal surface, sinistrally at the level of the intestinal bifurcation.

The large *ovary* (Fig. 13) is oval to lobate, lies between the ends of the caeca, pre-testicularly and often close to the ventral sucker. Mehlis' gland and the canalicular seminal receptacle lie posteriorly to the ovary, and Laurer's canal opens dorsally. The *uterine coils* lie mainly post-testicularly (Fig. 14), and the uterus may completely fill the post-testicular region (Figs 12c,i, 16B) or have an area of parenchyma surrounding it (Figs 12g,m, 16C). In the latter case, it is usual for a few slings to reach close to the body margin (Figs 12f,j, 16A). The numerous eggs are small, with strongly tanned, operculate shells and narrow strands of egg-shell-like material lie in the uterus. The *vitellarium* consists of two subsymmetrical fields of follicles lying between the testes and the ovary.

Discussion. Bray (1979) included his specimens from zoarcid teleosts *(Lycodes* spp.*)* in his list of hosts of *L. steenstrupi* from the eastern coastal regions of Canada. He mentioned that there appeared to be a host-induced effect on the morphology of the zoarcid forms which developed larger gonads and a more extensive uterus than the forms from *Anarhichas* spp., but that intermediate forms were present. Subsequent studies (see Bray & Rollinson, 1985) have shown the dangers in postulating host-induced variation without proof, so that it was felt that the features

listed above in the key and discussion were sufficient to distinguish this form from *L. steenstrupi* at the specific level. Other records of *L. steenstrupi* from zoarcids, i.e. those of Stafford (1904, 1907), Cooper (1915) and Linkletter *et al.* (1977), are all from *Macrozoarces americanus* from the Canadian east coast and, therefore, probably represent the same form as the one we have studied. The species is named for Dr R. G. Appy of the University of Guelph, Ontario, Canada.

Genus *PANOPULA* Overstreet & Pritchard, 1977

DIAGNOSTIC FEATURES. Body fusiform. Body surface spinous throughout. Oral sucker globular to infundibuliform. Oesophagus distinct. Caeca short, reaching to testes or just overlapping ventral sucker. Ventral sucker subequal or larger than oral sucker. Testes symmetrical, level with ventral sucker or in posterior hindbody. Cirrus-sac large, claviform. Seminal vesicle bipartite or coiled. Pars prostatica wide, vesicular. Ejaculatory duct muscular, long. Genital atrium simple, distinct. Genital pore sinistral, in mid-forebody, lateral or sublateral. Ovary globular to oval, smooth to irregular, post-testicular. Eggs tanned. Uterus post-testicular. Vitellarium two lateral fields of follicles in mid to posterior forebody. Excretory vesicle saccular. In intestine of deep-sea teleosts.

Key to *Panopula* spp. found in north-east Atlantic

1 Testes almost entirely in forebody. Sucker ratio 1 :> 1·5. Caeca overlapping testes . . . . . *P. bridgeri* sp. nov (p. 171)

— Testes lateral to ventral sucker. Sucker ratio 1 : < 1·25. Caeca not reaching testes . . . . . *P. spinosa* (Zubchenko, 1978) (p. 173)

Panopula bridgeri sp. nov.

TYPE-HOST AND LOCALITY. *Polyacanthonotus rissoanus,* off Tory Island, NW of Ireland (55°N, 10°W).

RECORDS

Material studied from NE Atlantic

Polyacanthonotus rissoanus [upper intestine] off Tory Island, NW of Ireland (55°N, 10°W; depth 800–1000 m; June, 1974). BM(NH) holotype 1982.12.8.1. paratypes 1982.12.8.2–5.

—— [——] St Kilda, W of Scotland (57°N, 09°W; depth 980–1030 m; June, 1974). BM(NH) paratypes 1982.12.8.6–7.

—— [——] East Rockall, W of Scotland (57°N,13°W; depth 1000–1020 m; June, 1974). BM(NH) paratypes 1982.12.8.8.

ASPECTS OF BIOLOGY. Virtually nothing is known of the biology of this parasite of deep-sea notacanthid eels. The above records indicate its known range. The related species *P. spinosa* (see below) occurs in a closely related eel.

PREVIOUS DESCRIPTIONS. None.

DESCRIPTION (Fig. 17). Fifteen specimens (one as sections) were studied. The measurements are given in Table 11. The mature worms are fusiform (Fig. 17A,B), bearing scale-like spines which reach just into the hindbody. The oval *oral sucker* opens subterminally with a somewhat slit-like opening and leads into a short prepharynx which is not always apparent in whole-mounts. A small, oval *pharynx* leads to a long, narrow oesophagus, which bifurcates at about the level of the genital pore, just anteriorly to the middle of the forebody. The caeca are short, but fairly narrow and reach back to about the level of the anterior margin of the ventral sucker and almost to the posterior edge of the testes, where they terminate blindly. The transversely elongate-oval *ventral sucker* lies in about the centre of the body and is larger than the oral sucker. It is rather weakly developed and is reduced to the form of a weakly-muscled pad rather than a sucker.

The *excretory pore* is terminal and leads into the vesicle which is in the form of a flattened sac reaching almost to the seminal receptacle.

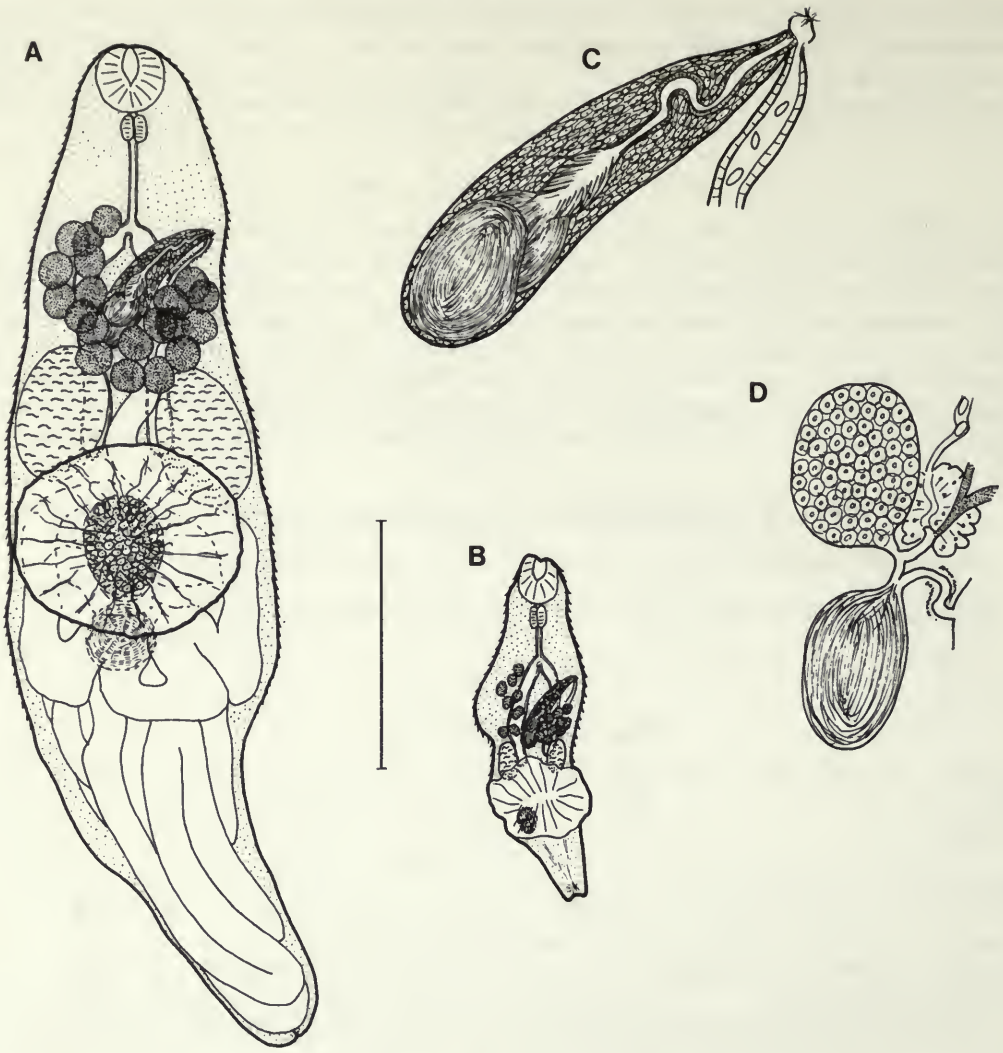

Fig. 17 *Panopula bridgeri* sp. nov. (A) Ventral view, mature worm; (B) Ventral view, immature worm; (C) Terminal genitalia; (D) Proximal female genitalia. Scale bar: A, B 0·5 mm.

The *testes* are smoothly or slightly irregularly oval, and lie extracaecally and subsymmetrically in the posterior forebody. The worm is clearly protandrous. The *cirrus-sac* is claviform and reaches posteriorly to about the anterior edge of the testes. It contains a seminal vesicle composed of two oval parts, a vesicular pars prostatica and a narrow, long, coiled or sinuous ejaculatory duct, which is sometimes extended to form a cirrus (Fig. 17C). It opens into a small, simple genital atrium which opens on the sinistrally submarginal ventral surface, just anterior to the middle of the forebody.

The oval *ovary* lies post-testicularly and dorsally to the ventral sucker. The oviduct passes posteriorly from the ovary and receives the duct from the canalicular seminal receptacle and Laurer's canal, and the common vitelline duct, before entering Mehlis' gland which lies sinistrally to the ovary. The large seminal receptacle lies posteriorly to the ovary and Laurer's canal arises from it. Laurer's canal is short, muscular and sinuous, opening dorsally at the level just posterior to the ovary (Fig. 17D). The *uterus* takes up nearly the whole of the post-testicular region of the worm (in the hindbody and dorsally to the ventral sucker) and contains numerous eggs with tanned,

Table 11 Measurements of *Panopula* spp.

	P. bridgeri	*P. spinosa*		
Authority	Present study	Zubchenko (1978)	Present study	
Locality	see text	2 localities	SW Iceland	NW Atlantic
Length (mm)	0·67–2·01	3·2–4·2	3·5	2·9
Breadth (mm)	0·22–0·55	1·1–1·5	1·15	1·4
Length : forebody ratio	1 : 0·39–0·56	–	1 : 0·53	1 : 0·54
Oral sucker (mm)	0·09–0·20 × 0·09–0·19	0·45–0·48	0·40 × 0·47	0·41 × 0·44
Ventral sucker (mm)	0·16–0·35 × 0·16–0·43	0·47–0·53 × 0·44–0·56	0·46 × 0·45	0·46 × 0·50
Sucker-ratio	1 : 1·5–2·8	–	1 : 0·96	1 : 1·14
Prepharynx (mm)	very short	0·03–0·04	0·02	0·06
Pharynx (mm)	0·04–0·07 × 0·04–0·07	0·21–0·27 × 0·19–0·21	0·21 × 0·22	0·21 × 0·19
Oesophagus (mm)	0·09–0·74	0·55–0·75	0·75	? 0·2 curved
Cirrus-sac (mm)	0·18–0·35 × 0·05–0·13	–	1·0 × 0·22	1·2 × 0·31
Testes (mm)	0·07–0·28 × 0·04–0·19	0·43–0·59 × 0·25–0·40	0·45–0·30	0·50–0·55 × 0·31–0·33
Ovary (mm)	0·06–0·20 0·08–0·17	0·25–0·35 × 0·25–0·32	0·26 × 0·24	0·31 × 0·30
Vitelline follicles				
poral	10–12	9–10	12	12
aporal	9–10		9	10
Eggs (μm)	36–40 × 15–17	33–38 × 13–17	33–36 × 15–17	33–36 × 16–17

operculate shells. A muscular metraterm enters the genital atrium beside the cirrus-sac. The *vitellarium* consists of two lateral bunches of subglobular follicles which almost meet in the median line posteriorly. The aporal field reaches from the intestinal bifurcation and overlaps the anterior edge of the testis posteriorly, but the poral field does not reach as far anteriorly, always being confined to the region postero-lateral to the cirrus-sac.

Discussion. This species clearly belongs in *Panopula,* as the testes lie in the forebody. The features which distinguish it from *P. spinosa* are mentioned in the key. As far as the type of the genus, *P. cavernossa* Overstreet & Pritchard, 1977, is concerned, the present species and *P. spinosa* can be distinguished by having the poral field of the vitellarium entirely posterior to the cirrus-sac and in having a bipartite, as opposed to a coiled, tubular, seminal vesicle. The species is named for Mr J. P. Bridger of the MAFF Laboratory, Lowestoft, Suffolk, England.

Panopula spinosa (Zubchenko, 1978) n. comb.

Antorchis spinosus Zubchenko, 1978.

Type-host and locality. *Notacanthus chemnitzii* [=*nasus*], Rejkjanes Ridge, SW Iceland.

Records

(i) Material studied
(a) From the NE Atlantic
Notacanthus chemnitzii [intestine] off SW Iceland (March, 1973). Donated by A. V. Gaevskaya. BM(NH) 1981.12.3.7.

(b) From elsewhere

Notacanthus chemnitzii [intestine] NW Atlantic (Nov., 1974). Donated by A. V. Gaevskaya. BM(NH) 1981.12.3.6.

(ii) NE Atlantic records from the literature

Notacanthus chemnitzii [intestine] northern part of Rejkjanes Ridge, off SW Iceland. Zubchenko (1978: 117 as *Antorchis spinosus*).

ASPECTS OF BIOLOGY. One host species only is recorded. Our specimens bear the information quoted for them and Zubchenko's (1978) locality information is more detailed. His record from the north-west Atlantic is from off Labrador.

PREVIOUS DESCRIPTIONS. Zubchenko (1978: 117).

DESCRIPTION (Fig. 18). Based on two flattened whole-mounts. The dimensions are included on Table 11. These elongate pyriform worms have an extensive forebody. The surface bears large spines which reach to the posterior extremity, becoming slightly more widely spaced posteriorly. The *oral sucker* is almost terminal, infundibuliform and leads through a short but distinct prepharynx to an oval *pharynx*. The oesophagus is long, either straight or curved depending on the extension of the forebody. It bifurcates in about the mid-forebody giving off short, saccular caeca which just reach to the vitelline fields. The rounded *ventral sucker* is slightly smaller to slightly larger than the oral sucker.

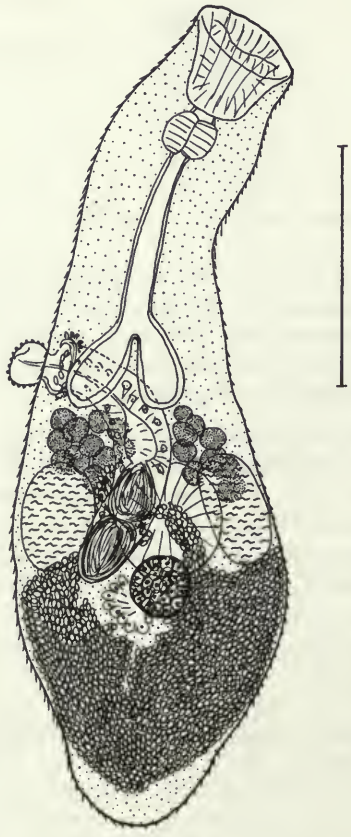

Fig. 18 *Panopula spinosa* (Zubchenko), dorsal view, flattened specimen from SW of Iceland. Scale bar: 1 mm.

The *excretory pore* is terminal and the excretory system is not clearly seen, but in the region posterior to the uterus, appears to be a broad sac.

The elongate oval *testes* lie laterally to antero-laterally to the ventral sucker in a more or less symmetrical arrangement. The large, curved *cirrus-sac* overlaps the ventral sucker to about the middle to the posterior edge. It contains a large seminal vesicle made up of two broadly oval parts, a wide, vesicular pars prostatica and a long, muscular ejaculatory duct which may form a large cirrus bearing numerous small bosses. The genital atrium is large, with muscular walls, and opens at or near the left lateral margin of the mid-forebody.

The round *ovary* lies submedially, post-testicularly and overlaps the posterior edge of the ventral sucker. Almost immediately posterior to it lies a small seminal receptacle, with a prominent Mehlis' gland to the left of the ovary. Laurer's canal was not visible on these flattened worms. The *uterus* fills most of the post-testicular and post-ovarian space and contains numerous thick-shelled, operculate eggs. The strongly muscular metraterm opens into the base of the genital atrium. The *vitellarium* consists of two small lateral fields of follicles lying immediately anterior to the testes on either side.

DISCUSSION. We believe that this species is clearly a zoogonid, not a fellodistomid as suggested by Zubchenko (1978). Although in some ways similar to *Antorchis* spp., the sublateral genital pore, large tegumental spines and apparently undivided excretory vesicle clearly associate it with the zoogonids, and the location of the testes and vitellarium, the structure of the intestine and the host suggest affinities with the genus *Panopula*.

Genus ***BRACHYENTERON*** Manter, 1934

Cypseluritrematoides Yamaguti, 1970.
Prolateroporus Yamaguti, 1971.

DIAGNOSTIC FEATURES. Body fusiform to pyriform. Body surface spinous. Oral sucker globular or infundibuliform. Oesophagus distinct. Caeca terminating in forebody or at level of ventral sucker. Ventral sucker in mid-body or just anterior; larger than or subequal to oral sucker, may have tegumental pit on posterior lip. Testes symmetrical or subsymmetrical, close to or overlapping ventral sucker. Cirrus-sac claviform to elongate claviform. Seminal vesicle bipartite or coiled. Pars prostatica vesicular, oval to elongate. Cirrus long, may be extruded. Genital pore marginal to submarginal, sinistral in forebody. Ovary overlapping ventral sucker or in forebody, pre- or post-testicular. Uterus fills most of hindbody. Metraterm well developed. Vitellarium lateral fields of follicles in forebody or at level of ventral sucker. Excretory vesicle elongate saccular. In gall-bladder or intestine of marine teleosts.

Key to *Brachyenteron* spp. found in the north-east Atlantic

1 Sucker ratio 1 : 2. Genital pore at level of pharynx. Tegumental pit on posterior lip of ventral sucker. Oral sucker subglobular . . . . . *B. pycnorganum* (Rees, 1953) (p. 175)
— Sucker ratio 1 : 1. Genital pore at level of intestinal bifurcation. No tegumental pit seen. Oral sucker infundibuliform . . . . . *B. campbelli* sp. nov. (p. 179)

Brachyenteron pycnorganum (Rees, 1953) Overstreet & Pritchard, 1977

Steganoderma pycnorganum Rees, 1953.
Deretrema pycnorganum (Rees, 1953) Yamaguti, 1953.
Steganoderma spinosa Polyansky, 1955.
Pseudochetosoma spinosa (Polyansky, 1955) Yamaguti, 1971.
Brachyenteron spinosum (Polyansky, 1955) Overstreet & Pritchard, 1977.
Yamagutia anarhichae Brinkmann, 1956.
Prolateroporus anarhichae (Brinkmann, 1956) Yamaguti, 1971.

TYPE-HOST AND LOCALITY. *Anarhichas minor*, Iceland.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Anarhichas denticulatus [gall-bladder, bile-duct] Iceland–Faeroes Channel (64°N, 10°W; depth 592–620 m; June, 1974). BM(NH) 1982.12.9.18–40.

Anarhichas lupus [bile-duct] northern North Sea. (61°N, 02°E; depth 159 m; May, 1985). BM(NH) 1985.7.3.16.

Anarhichas minor [bile-duct] east coast of Iceland (66°N, 13°W; depth 119 m.) Material of G. Rees (possibly type, but not labelled as such). (See Rees, 1953:21). BM(NH) 1976.4.9.16.

—— [gall-bladder] Neskaupstadur, Iceland. Material lent by Museum of Natural History, Rejkjavik. Type-specimen of *Yamagutia anarhichae*. (See Brinkmann, 1956: 17; Bray & Gibson, 1980: 202).

—— [——] Anton Dohrn Bank (65°N, 30°W; depth 370–440 m; May, 1974). BM(NH) 1982.12.9.4–13.

—— [gall-bladder, bile-duct] Iceland–Faeroes Channel (63°N, 11°W; depth 410–420 m; June, 1974). BM(NH) 1982.12.9.14–17.

(b) From elsewhere

Anarhichas lupus [gall-bladder] off Nova Scotia. (See Bray, 1979: 418; as *Deretrema p.*). BM(NH) 1977.2.15.103–110.

Anarhichas minor [gall-bladder] off Newfoundland. (See Bray, 1979: 418; as *Deretrema p.*). BM(NH) 1977.2.15.111.

(ii) NE Atlantic records from the literature

Anarhichas minor [bile-duct] east coast of Iceland. Rees (1953: 21; Brinkmann (1956) erroneously quotes this record as from *A. lupus*).

—— [gall-bladder] Neskaupstadur and Húsavík, Iceland. Brinkmann (1956: 16; as *S. pycnorganum:* 17; as *Yamagutia anarhichae*).

ASPECTS OF BIOLOGY. Nothing is known of the life-cycle of this worm, but it is worth noting that metacercariae allocated to the related species *B. doederleiniae* Yamaguti, 1938 have been found in deep water and red shrimps by Reimer (1984). *B. pycnorganum* is found almost exclusively in the gall-bladder and bile-duct of *Anarhichas* spp. in the north Atlantic Ocean. Polyansky recorded nine specimens in the intestine in 1 of 15 specimens of *A. lupus* in the Barents Sea. It appears to occupy the niches occupied by *Fellodistomum fellis* (Olsson, 1868) and possibly *Steringophorus agnotus* (Nicoll, 1909) in *A. lupus* (see Bray & Gibson, 1980) but is sometimes found sympatrically with *F. fellis* in *A. minor* (see Brinkmann, 1956, 1975; Bray, 1979).

PREVIOUS DESCRIPTIONS. Rees (1953: 21); Brinkmann (1956: 16, 17); Polyansky (1955: 58).

DESCRIPTION (Figs 19, 20). Five worms, three in serial section were studied. Their dimensions are included in Table 12. They are somewhat fusiform, with the forebody being asymmetrical due to the genital pore being carried on a slight eminence (Fig. 19A). The surface normally bears small spines embedded in the tegument over almost the entire surface, often with only the tips showing through. A distinct tegumental pit lies on the median line close to the posterior border of the opening of the oral sucker. It is seen clearly only on SEM preparations (Fig. 20). The globular *oral sucker* opens subterminally, and leads via a short prepharynx and a small subglobular *pharynx* into a distinct oesophagus, lined with tegument, which bifurcates in the posterior forebody. The short, wide, divergent caeca reach to about the middle of the ventral sucker. Most of each caecum is lined with epithelium, with tegumental lining occurring only anteriorly. The large, circular *ventral sucker*, normally about twice the width of the oral sucker, lies in the middle of the worm.

The *excretory pore* lies terminally and leads to a narrow, I-shaped undivided vesicle reaching to the level of the seminal receptacle.

Large, oval *testes* lie more or less symmetrically in the anterior hindbody. The *cirrus-sac* is large, usually recurved sharply (in unflattened material) and has a strongly muscular wall. It reaches posteriorly to a level between about the middle of the ventral sucker to well within the hindbody (Fig. 19A,B). Proximally, the cirrus-sac contains a large, bipartite seminal vesicle; the two broadly oval parts have muscular walls which may be lined with a single layer of anuclear blebs. The vesicular pars prostatica is lined with filaments which project into the lumen and are embedded in

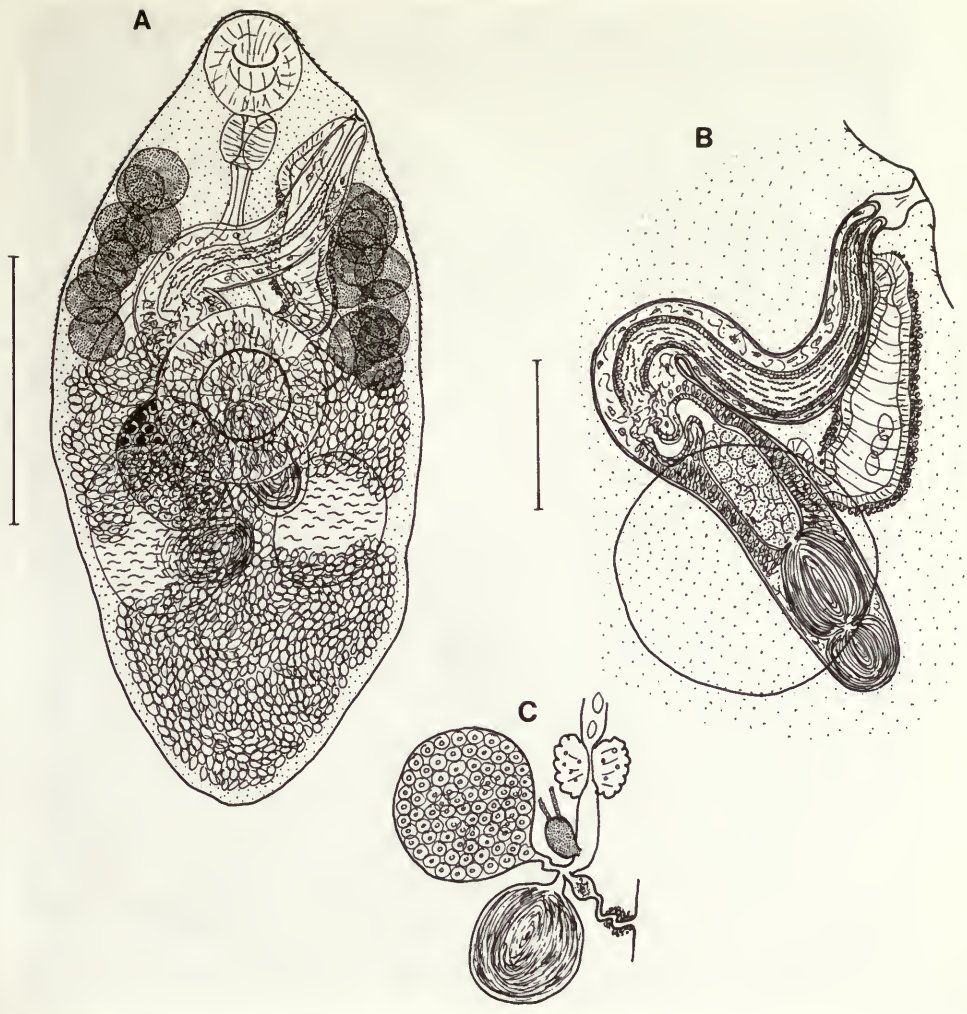

Fig. 19 *Brachyenteron pycnorganum* (Rees). (A) Ventral view, ex *Anarhichas minor*; (B) Terminal genitalia; (C) Proximal female genitalia. Scale bars: A 0·5 mm, B 0·2 mm.

the granular matrix. Prior to the point where the cirrus-sac curves sharply, the ejaculatory duct has its origin. It is distinguishable from the pars prostatica by its initially narrower lumen and thicker muscular wall. Its inner surface is covered with muscular tubercles. The pars prostatica and the proximal part of the ejaculatory duct are surrounded by a layer of gland-cells. At about the point of recurvature the gland-cell layer more or less disappears, leaving a narrow layer of connective tissue, containing an occasional gland-cell, between the thick muscular ejaculatory duct and the thinner, but still strongly muscular, wall of the cirrus-sac. The ejaculatory duct may be extruded to form a cirrus, which is usually short (see fig. 23c of Polyansky, 1955) and covered with tubercles. When the worm is flattened (see Rees, 1953, fig. 2) the cirrus may be almost completely extended and the relative positions and shape of some of the contents of the cirrus-sac may be substantially altered, as may the shape of the cirrus-sac itself. The withdrawn cirrus opens into the base of a distinct, narrow, genital atrium which opens on a slight eminence on the left margin of the forebody at the level of the pharynx.

The oval *ovary* lies on, or to the right of, the median line, overlapping the posterior margin of the ventral sucker and is either pre-testicular or overlaps the testes. The narrow oviduct passes from

Fig. 20 *Brachyenteron pycnorganum* (Rees). SEM micrograph showing tegumental pit (arrowed). Scale bar: 0·2 mm.

the left dorsal side of the ovary, receiving the ducts of the canalicular seminal receptacle and the vitelline system before passing into a small Mehlis' gland lying sinistrally to the ovary. The seminal receptacle lies more or less directly posterior to the ovary and may be nearly as large. Laurer's canal passes dorsally from the seminal receptacle arising close to its junction with the oviduct (Fig. 19C). Initially it is dilate and contains a small amount of apparently spent spermatozoa and vitelline material. Distally it is narrow, convoluted and ensheathed in a narrow layer of gland-cells. It opens dorsally at about the level of the seminal receptacle. The *uterus,* on leaving Mehlis' gland anteriorly, curves posteriorly and coils throughout most of the hindbody, both anteriorly and posteriorly to the testes. It contains numerous operculate, tanned eggs with numerous fine filaments. The metraterm is long, strongly muscular and surrounded by a layer of gland cells. It commences dorsally to the ventral sucker and runs a convoluted course to enter the genital atrium dorsally to the cirrus-sac. The common vitelline duct widens to form a reservoir almost immediately on leaving the oviduct. Two narrow ducts pass from the reservoir towards the *vitellarium*, which consists of two subsymmetrical lateral fields of globular follicles in the forebody, but posterior to the cirrus-sac on the poral side. The fields reach from a level just posterior to the cirrus-sac to about the middle of the ovary.

Table 12 Measurements of *Brachyenteron* spp.

	B. pycnorganum				*B. campbelli*
Authority	Rees (1953)	Polyansky (1955)	Brinkmann (1956)	Present study	Present study
Length (mm)	2·44–2·82	1·87–1·2	1·04	0·94–2·1	2·1
Breadth (mm)	1·41–1·52	0·87–1·2	0·49	0·37–0·98	0·43
Length : forebody ratio	–	–	–	1 : 0·32–0·44	1 : 0·36
Oral sucker (mm)	0·36 × 0·34	0·29–0·37	0·13 diam.	0·14–0·28 × 0·12–0·29	0·22 × 0·17
Ventral sucker (mm)	0·62 diam.	0·42–0·50	0·32 diam.	0·24–0·55 × 0·24–0·58	0·11 × 0·17
Sucker-ratio	1 : 1·85	[1 : 1·2–1·3]*	1 : 2·45	1 : 1·6–2·0	1 : 1
Pharynx (mm)	0·14 diam.	0·11–0·14 diam.	0·06 diam.	0·05–0·16 × 0·06–0·16	0·11 × 0·08
Oesophagus (mm)	0·20	0·12	–	0·06–0·23	*c.* 0·09
Cirrus-sac (mm)	0·98 × 0·26	1·04–1·37 long	0·55 long	0·48–1·52 × 0·10–0·20	0·51 × 0·09
Testes (mm)	0·27–0·38 × 0·23–0·33	0·19–0·25 × 0·30–0·40	–	0·12–0·42 × 0·09–0·36	0·19–0·22 × 0·13
Ovary (mm)	0·25 diam.	0·17–0·25 diam.	–	0·08–0·32 × 0·06–0·22	0·20 × 0·12
Vitelline follicles					
poral	10–12	9–12	–	11–14	10
aporal	8–11			8–13	9
Eggs (μm)	31–38 × 19–20	29–34 × 16–21	40 × 25	34–40 × 18–24	32–33 × 14–17

*Taken from published figure.

Discussion. Brinkmann (1956) was the first to consider *Steganoderma spinosa* a synonym of *S. pycnorganum*. Overstreet & Pritchard (1977), however, pointed out that *S. spinosa* apparently differs from *S. pycnorganum* in lacking a 'well-developed metraterm-complex'. We believe that, despite this fact, and the finding of *S. spinosa* in the intestine of *A. lupus*, the overall morphology is so similar that it is apparent that we are dealing with a single sub-arctic form. Zubchenko (1980) recorded *S. spinosa* from *A. minor* in the north-west Atlantic, and our specimens from this host and region are clearly *B. pycnorganum*.

As mentioned by Bray & Gibson (1980) we have examined the single specimen of *Yamagutia anarhichae* Brinkmann, 1956, and consider it a teratological specimen of *Brachyenteron pycnorganum*.

Brachyenteron campbelli sp. nov.

Type-host and locality. *Polyacanthonotus rissoanus*, 58°N, 10°W.

Records

(i) Material studied from the NE Atlantic region
Polyacanthonotus rissoanus [intestine] NW off Scotland (58°N, 10°W; depth 1300–1320 m; Oct., 1978). BM(NH) holotype 1981.2.18.1.

(ii) NE Atlantic records from the literature
None.

Previous descriptions. None.

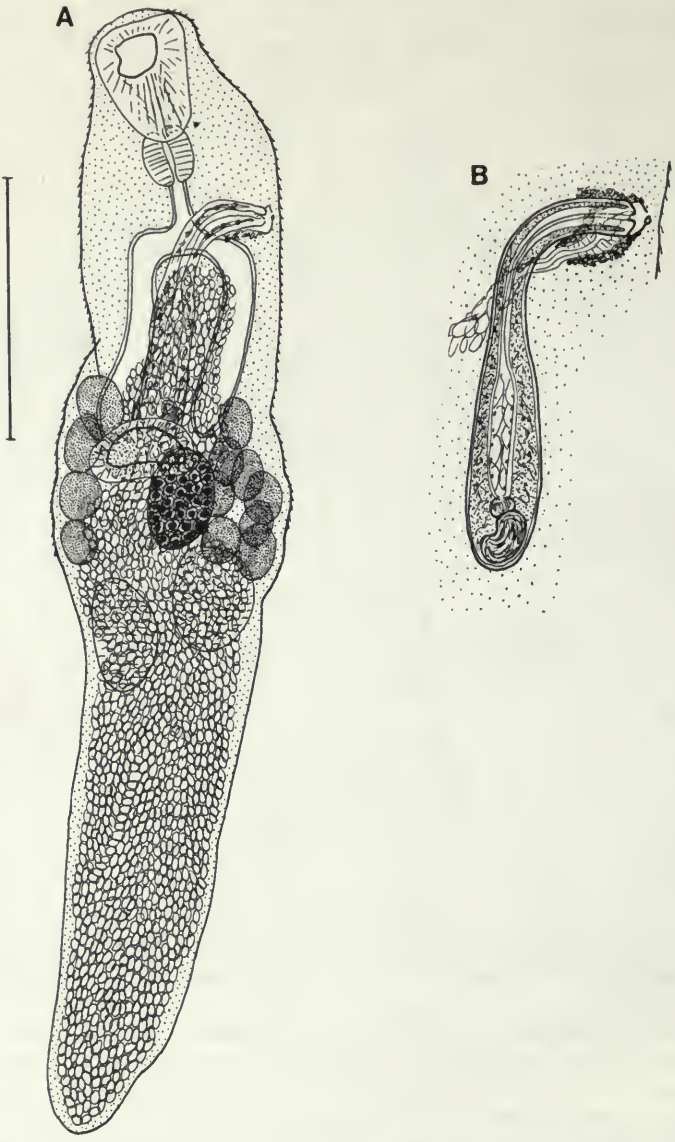

Fig. 21 *Brachyenteron campbelli* sp. nov. (A) Ventral view; (B) Terminal genitalia. Scale bar: 0·5 mm.

DESCRIPTION (Fig. 21). Only a single worm was recovered and its measurements are given on Table 12. It has been examined in whole-mount preparation and as serial sections. Certain details, particularly of the proximal female system, were not clearly seen. The worm is elongate (Fig. 21A), and the surface bears spines to the level of the anterior part of the hindbody. It is widest at the level of the ventral sucker and vitellarium, and the contours of the lateral margins of this region reflect the outlines of the underlying vitelline follicles. The infundibuliform oral sucker leads via a short prepharynx to an oval *pharynx* and a distinct oesophagus which divides in about the middle of the forebody. The caeca are narrow and fairly short, terminating at the level of the ventral sucker, which is relatively weakly developed and lies in the anterior half of the body.

The *excretory pore* is dorsally subterminal and leads to a narrow vesicle which reaches to the gonads.

The *testes* are oval and lie slightly obliquely in the anterior hindbody, with the anterior testis on the poral side of the body, close to the ovary. The *cirrus-sac* is a long, narrow, claviform organ curved at a right-angle at its anterior end (Fig. 21B). It contains a small, bipartite seminal vesicle, made up of a larger slightly elongate proximal part and a small globular distal part. A long, vesicular pars prostatica reaches to about half-way to the point of curvature and leads to a long, muscular ejaculatory duct. The genital atrium is small, but distinct, muscular and surrounded by gland-cells, as are the distal regions of the cirrus-sac and particularly the metraterm. The pore opens ventrally close to the sinistral margin at the level of the oesophagus.

The oval *ovary* lies more or less on the median line, overlapping the posterior edge of the ventral sucker. The seminal receptacle is smaller than the ovary and overlaps it postero-dorsally. Laurer's canal was not clearly seen, but apparently opens dorsally at the level of the testes. The *uterus,* distended with operculate eggs, fills most of the hindbody and also lies in the median region of the forebody, between the caeca. The post-testicular eggs are relatively weakly tanned compared with those in the pre-testicular region. The strongly muscular metraterm enters the genital atrium dorsally to the cirrus-sac and is surrounded by a thick layer of gland-cells. The *vitellarium* consists of oval follicles in fields lateral to the region around the ventral sucker, but overlapping into both the fore and hindbodies.

DISCUSSION. This is one of the occasions when, despite having but one specimen available, it is practically certain that we are dealing with a new form. It is the only member of the genus to possess an infundibuliform oral sucker and a uterus which reaches anteriorly to the testes and into the forebody. The species is named for Dr R. A. Campbell of Southeastern Massachusetts University, North Dartmouth, Massachusetts, USA.

Genus *STEGANODERMATOIDES* Parukhin & Lyadov, 1979

Hudsonia Campbell, 1975 *nec* Edwards, 1923.
Allosteganoderma Campbell, 1983.

DIAGNOSTIC FEATURES. Body fusiform to elongate fusiform, bearing prominent spines. Oral sucker terminal or subterminal. Prepharynx distinct. Oesophagus long. Caeca reach to testis level. Ventral sucker large, in about middle of body, bearing equatorial row of large, muscular papillae. Testes diagonal in mid to posterior hindbody. Cirrus-sac large, recurved. Seminal vesicle saccular, bipartite or convoluted tubular. Pars prostatica long, convoluted. Ejaculatory duct muscular. Genital atrium large, muscular. Periatrial gland present, undivided. Genital pore sinistral, lateral in mid-posterior forebody. Ovary submedian, pre-testicular. Uterus substantially or totally pre-testicular. Metraterm muscular, surrounded by gland-cell sheath. Vitelline follicles in two lateral fields in anterior hindbody. Excretory vesicle reaches to testes or not. In alimentary system of deep-sea teleosts.

COMMENTS. This genus is discussed in detail by Bray (1985*a* and in press *b*). One species is found in the north-east Atlantic.

Steganodermatoides maceri sp. nov.

? *Hudsonia agassizi* from *Alepocephalus bairdii* of Zubchenko (1984).

TYPE-HOST AND LOCALITY. *Alepocephalus bairdii,* off Tory Island, W of Ireland.

RECORDS

(i) Material studied from the NE Atlantic region
Alepocephalus bairdii [rectum] off Tory Island, W. of Ireland, (55°N, 10°W; depth 800–840 m; and 55°N, 11°W; depth 800–820 m, April, 1973). BM(NH) Holotype 1984.2.23.1. Paratypes 1984.2.23.2–8.
—— [——] St Kilda, off W. of Scotland. (57°N, 10°W; depth 650–660 m and 800–830 m; June, 1974). BM(NH) Paratypes 1984.2.23.9–11.
—— [——] Porcupine Bank, off W. Ireland. (54°N, 14°W; depth 1000 m; June, 1974). BM(NH) Paratypes 1984.2.23.12.
—— [——] South Rockall, off W. Scotland (55°N, 17°W; depth 821–850 m; June, 1974). BM(NH) Paratype 1984.2.23.13.

—— [——] East Rockall, off W. Scotland (57°N, 13°W; depth 1000–1060 m; June, 1974). BM(NH) Paratypes 1984.2.23.14–20.

—— [——] Sulisker, off NW Scotland (60°N, 07°W; depth 900 m; June, 1974). BM(NH) Paratypes 1984.2.23.21. (59°N, 08°W; depth 1160–1220 m; Oct., 1978). BM(NH) Paratypes 1984.2.23.22–23.

—— [——] Flannan, off NW Scotland (59°N, 09°W; depth 1000 m; Oct., 1978). BM(NH) Paratype 1984.2.23.24.

(ii) NE Atlantic records from the literature

Alepocephalus bairdii [?] North-east Atlantic. Zubchenko (1984: 78, as *Hudsonia agassizi*-likely to be *S. maceri*).

ASPECTS OF BIOLOGY. This species is clearly both host-specific to *A. bairdii* and site-specific to the rectum. Nothing is known of the life-history or wider distribution.

PREVIOUS DESCRIPTIONS. None.

DESCRIPTION (Figs 22, 23). Thirty-eight specimens, including one set of serial sections, were studied. The measurements are given on Table 13. The worms are elongate, widest at about the level of the ventral sucker, or in larger worms just posterior to the ventral sucker (Fig. 22A). The forebody is narrow, being constricted just posteriorly to the oral sucker and gradually widening towards the ventral sucker. The hindbody is elongate, wider anteriorly and tapering to a narrow, pointed end. The surface bears large spines, the only parts lacking these spines being a narrow band around the oral sucker (Fig. 23A) and the posterior extremity. The large *oral sucker* opens subterminally to virtually terminally. It is more or less globular and leads via a distinct prepharynx to an oval *pharynx* which is often orientated obliquely and apparently distorted (Fig. 22A). A long, sinuous oesophagus reaches just into the posterior half of the forebody where it bifurcates, giving rise to two narrow caeca which diverge and, passing close to the lateral margin of the body, reach to about the level of the anterior margin of the posterior testis. The large *ventral sucker* lies in about the centre of the body. It tends to have a rather angular shape, rather than being circular, and across its internal equator there lies a row of about five or six large, fungiform papillae (Fig. 23B).

The terminal *excretory pore* leads into a narrow vesicle which reaches about half-way to the posterior testis in larger worms, lying dorsally to the uterus. In younger worms it may reach to, but not overlap, the testes.

The *testes* lie close together, diagonally in about the middle of the hindbody. They are oval to pyriform with more or less smooth margins. The *cirrus-sac* is a large recurved or coiled organ, with strong muscular walls, reaching from a level dorsal to the anterior half of the ventral sucker to the sinistrally placed genital atrium (Fig. 22B). The seminal vesicle is bipartite. The proximal part is saccular or tubular and smaller than the large, oval distal part, to which it is connected by a short, narrow canal. The long, convoluted vesicular pars prostatica is lined with a layer of large, anuclear blebs or globules, and passes through a mass of gland-cells. The male duct forms, distally, a narrow, muscular ejaculatory duct, lined with muscular annuli. It may extend through the genital pore as a wide blunt cirrus or be withdrawn into the proximal part of the cirrus-sac. When the cirrus is extended the genital atrium forms a strongly muscular sucker-like protuberance, and it appears that spermatophores may be formed. The genital atrium in resting condition is large and pocketed with a strong muscular wall lined with long filamentous structures reaching well into the lumen. The so-called periatrial gland surrounds the genital atrium and extends along the metraterm (Fig. 22B). It appears to be delimited by a membranous layer or parenchymatous capsule. The genital pore lies on the sinistral margin just posteriorly to the intestinal bifurcation.

The large, oval *ovary* lies anteriorly to the testes, usually closer to them than to the ventral sucker and more or less in the median line. The oviduct passes from the ovary close to its posterior end and soon receives both the common duct from Laurer's canal and the canalicular seminal receptacle and the common vitelline duct (Fig. 22C); then it enters Mehlis' gland. The seminal receptacle lies directly posterior to the ovary, lying anteriorly to or overlapping the anterior testis. It may be larger than the ovary when fully distended. Laurer's canal passes from the anterior edge of the seminal receptacle and is a short, convoluted tube opening dorsally at the level of the ovary. The vitelline connecting ducts join close to Mehlis' gland to form a small reservoir which is connected to

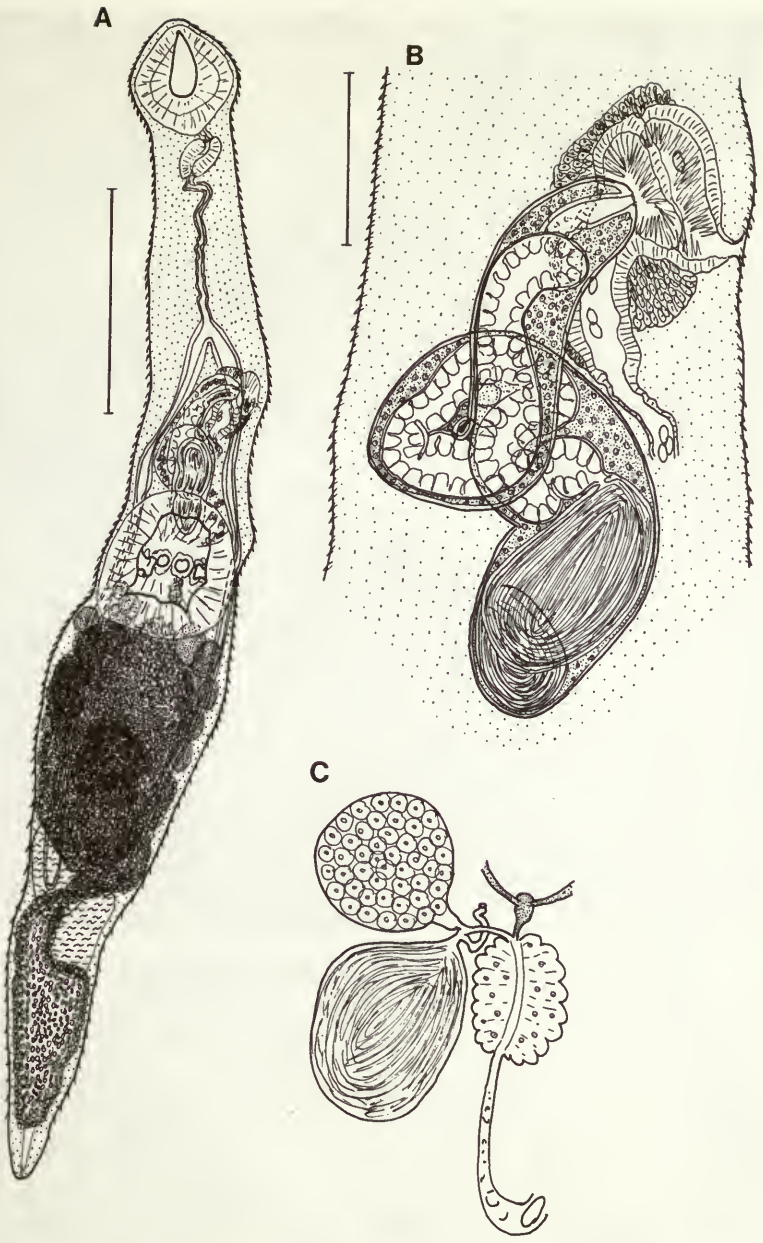

Fig. 22 *Steganodermatoides maceri* sp. nov. (A) Ventral view; (B) Terminal genitalia; (C) Proximal female genitalia. Scale bars: A 1 mm, B 0·2 mm.

the oviduct by a narrow common duct. The initial sling of the *uterus* passes posteriorly from Mehlis' gland and contains components of the eggs, but it is not clear where they are assembled so a uterine oötype may be present. The uterus passes into the post-testicular region. All specimens have at least some slings in this region and in larger worms a substantial part of the uterus is post-testicular. Eggs in the post-testicular part of the uterus are weakly tanned, and as the uterus passes the level of the testes going anteriorly, the eggs become fully tanned and may obscure the gonads. The uterus is convoluted between the testes and the ventral sucker and a narrow,

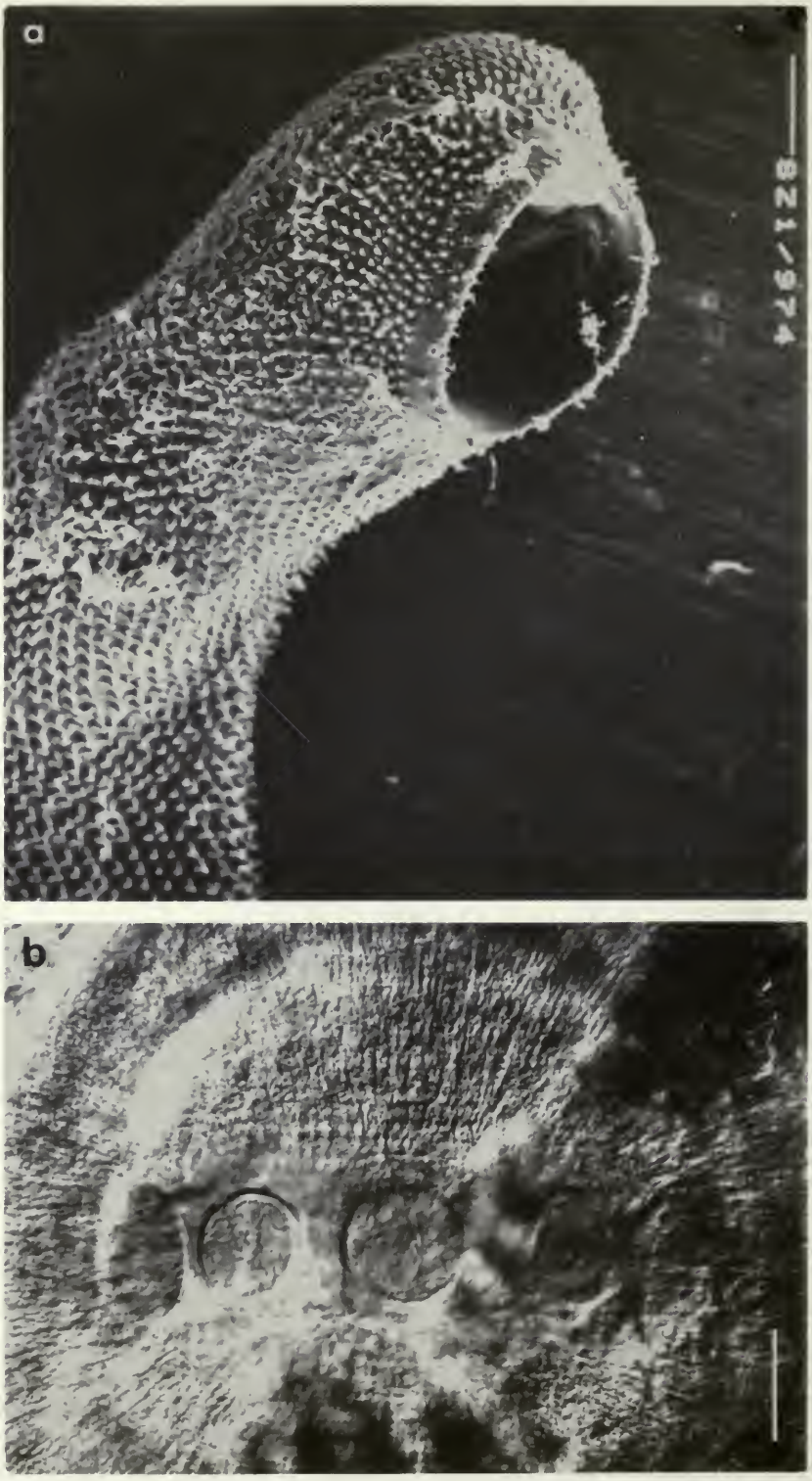

Fig. 23 *Steganodermatoides maceri* sp. nov. (a) SEM micrograph of the anterior end; (b) Optical photomicrograph showing papillae in ventral sucker. Scale bars: a, b 0·01 mm.

Table 13 Measurements of *Neosteganoderma glandulosum* and *Steganodermatoides maceri*

	N. glandulosum			*S. maceri*
Authority	Byrd (1964)	Bray (1973)	Yamaguti (1970)	Present study
Length (mm)	1·80–3·42	1·0–1·38	2·2–2·5	3·75–6·2
Breadth (mm)	0·74–1·26	0·76–0·96	0·85–1·7	0·55–1·1
Length : forebody ratio	[1 : 0·49–0·51]*	1 : 0·26–0·38	[1 : 0·47]*	1 : 0·35–0·47
Oral sucker (mm)	0·19–0·23 wide	0·26–0·33 × 0·27–0·38	0·20–0·25 × 0·20–0·27	0·38–0·60 diam.
Ventral sucker (mm)	0·24–1·22 wide	0·27–0·33 × 0·69–0·77	0·25–0·32 × 0·57–0·78	0·53–0·65 × 0·48–0·98
Sucker-ratio	1 : 3·9–1·6	1 : 2·1–2·8	[1 : 3]*	1 : 1·18–1·64
Prepharynx (mm)	–	–	–	0·02–0·05
Pharynx (mm)	0·06–0·10 × 0·06–0·09	0·11–0·13 diam.	0·08–0·09 × 0·05–0·08	0·13–0·25 × 0·12–0·19
Oesophagus (mm)	0·50–0·98	–	0·15–0·20	0·52–0·90
Cirrus-sac (mm)	–	0·94–1·01 × 0·15–0·30	0·52–0·60 × 0·12–0·14	0·80–1·25 × 0·17–0·23
Testes (mm)	0·24–0·47 × 0·25–0·43	0·19–0·30 × 0·27–0·40	0·25–0·30 × 0·15–0·18	0·30–0·80 × 0·17–0·50
Ovary (mm)	0·21–0·27 × 0·19–0·25	0·27 × 0·27	0·13 × 0·12	0·25–0·30 × 0·17–0·30
Eggs (μm)	26–31 × 12–15	26–31 × 16–21	25–35 × 16–20	28–33 × 14–19

*Taken from published figure.

convoluted sling passes dorsally to the latter. The uterine wall widens about half-way between the ventral sucker and the genital atrium forming a metraterm which is a strongly muscular, wide tube surrounded by a prominent glandular sheath and which opens into the dorsal part of the genital atrium. The *vitellarium* consists of two lateral fields of about 15 follicles extending between about the posterior margin of the ventral sucker and the ovary.

Discussion. This species differs from the three previously described members of the genus, *S. kergeleni* Parukhin & Lyadov, 1979, *S. allocytti* (Tkachuk, 1979) and *S. agassizi* (Campbell, 1975) by having a conspicuous post-testicular uterine development. This means that the testes are relatively further forward in *S. maceri* and the excretory vesicle does not always reach to the testes, as it does in the other species. The eggs of *S. maceri* (28–33 μm) are distinctly smaller than those of *S. agassizi* (48–55 μm). The species is named for Dr C. T. Macer of the MAFF Laboratory, Lowestoft, Suffolk, England.

Genus *NEOSTEGANODERMA* Byrd, 1964

Diagnostic features. Body pyriform, surface spinous. Oral sucker large, globular or infundibuliform. Prepharynx short. Oesophagus distinct. Caeca reach to testes, or almost so. Ventral sucker large, transversely elongate; divided equatorially by dorsal cleft and ventral ridge. Testes symmetrical in anterior hindbody. Cirrus-sac large, muscular. Seminal vesicle convoluted tubular. Pars prostatica long, wide. Ejaculatory duct muscular. Genital atrium large, pocketed. Periatrial gland present, undivided. Genital pore submarginal, sinistral, in posterior forebody. Ovary globular, inter-testicular. Uterus mainly post-testicular. Eggs tanned, opercular. Metraterm muscular. Vitellarium two small lateral fields of follicles, in anterior hindbody, pre-testicular.

Excretory pore terminal or dorsally subterminal; vesicle an elongate sac. In intestine of deep-sea teleosts.

COMMENT. One species is found in the north-east Atlantic.

Neosteganoderma glandulosum Byrd, 1964

Proctophantastes glandulosa (Byrd, 1964) Yamaguti, 1971.
Proctophantastes polymixiae Yamaguti, 1970.
Neosteganoderma polymixiae (Yamaguti, 1970) Bray, 1973.

TYPE-HOST AND LOCALITY. *Polymixia lowei*, Straits of Florida.

RECORDS

(i) Material studied
(a) From the NE Atlantic region
Beryx decadactylus [intestine] SW Bay of Biscay (44°N, 07°W; depth 340–350 m; Jan., 1971). Material of Bray (1973: 170). BM(NH) 1973.5.17.54–56.

(b) From elsewhere
Polymixia japonica [intestine] Hawaii. Holotype and paratype of *Proctophantastes polymixiae*. USNM 63568.
Polymixia lowei [lower intestine] Straits of Florida. Paratype. USNM 60166.

(ii) NE Atlantic records from the literature
Beryx decadactylus [intestine] SW Bay of Biscay. Bray (1973: 170).

ASPECTS OF BIOLOGY. Nothing is known of the life-history of this species. It occurs in fishes of the genera *Polymixia, Beryx, Cyttoidops* and *Cyttus* from Florida, the Bay of Biscay, Hawaii and the Australia–New Zealand region.

PREVIOUS DESCRIPTIONS. Byrd (1964: 105); Bray (1973: 170); Yamaguti (1970: 35).

DESCRIPTION (Figs 24, 25). Ten specimens from *B. decadactylus* were studied, one in serial section, together with one whole-mount from *P. lowei* and two whole-mounts from *P. japonica*. The dimensions are given on Table 13. When contracted the worms have a broadly pyriform outline (see Bray, 1973, fig. 8a) but when relaxed thay are more elongate (Fig. 24A). Quincunxially arranged acuminate spines are distributed throughout the surface of the forebody and a few spines are to be found at the posterior extremity. The subterminal *oral sucker* leads through a small prepharynx and a globular *pharynx* to a distinct, dorsally-curved, oesophagus which bifurcates close behind the pharynx to form caeca which reach back just dorsally to the testes. The large, muscular, transversely elongate *ventral sucker* is almost as wide as the body, and in these contracted specimens, lies in the anterior half of the body. It is divided equatorially by a cleft in the dorsal surface of the musculature and a corresponding ridge across the inner, ventral surface (Fig. 25A).

The *excretory system* was seen only in the sectioned specimen and in this case the pore was subterminally on the dorsal surface, possibly displaced by either the enlargement of the uterus or the contraction during fixation. Initially narrow, the vesicle widens anteriorly and terminates as a sac ventrally to the seminal receptacle.

The large *testes* are obscured by eggs in whole-mounts, but apparently lie symmetrically just posterior to the ventral sucker and close to the lateral margins of the worm. The *cirrus-sac* is very large with well-developed muscular walls. It is strongly recurved with the proximal part curved round dorsally to the distal part, which lies transversely across the worm overlapping the anterior margin of the ventral sucker (Fig. 24B). The proximal part reaches from close to the aporal margin nearly to the median region. The seminal vesicle is in the form of a tightly coiled tube and takes up a relatively small proportion of the cirrus-sac. The main part of the male duct within the cirrus-sac is the pars prostatica, which is lined with numerous, closely packed filamentous projections. The ejaculatory duct is wide with prominent muscular walls, and, at about its middle, a radial layer of hyaline spine-like structures may be seen. It is not clear whether these are, in fact, spines or fragments of longitudinal muscle. The male duct within the cirrus-sac is surrounded by numerous

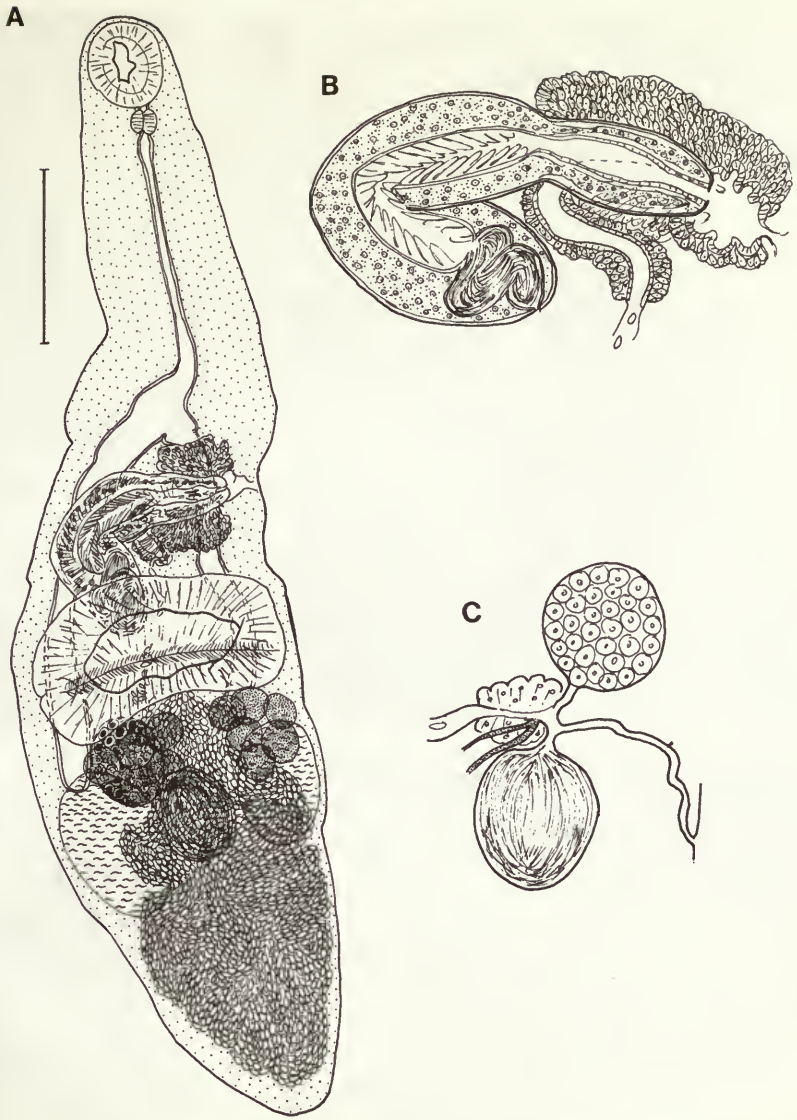

Fig. 24 *Neosteganoderma glandulosum* Byrd. (A) Ventral view of paratype specimen; (B) Terminal genitalia of specimen ex *Beryx decadactylus*; (C) Proximal female genitalia of specimen ex *B. decadactylus*. Scale bar: 0·5 mm.

gland-cells. The genital atrium has a thick, muscular wall, thrown into complex pockets and ridges, and opens via a narrow genital pore submarginally, close to the left margin of the posterior forebody. The genital atrium is surrounded by a thick layer of gland-cells which forms a sheath surrounding not only the genital atrium but also the distal end of the cirrus-sac and a considerable length of the metraterm. This glandular mass is distinctly delimited from the parenchyma and apparently forms a discrete organ which has been called a 'periatrial gland' (Yamaguti, 1970) (Fig. 25b).

The subglobular to irregularly quadrilateral *ovary* lies aporally to the median line between the testes. It gives off from its left margin a muscular oviduct which almost immediately enters a well-developed Mehlis' gland. A narrow duct passes dorsally leading to a large, oval canalicular

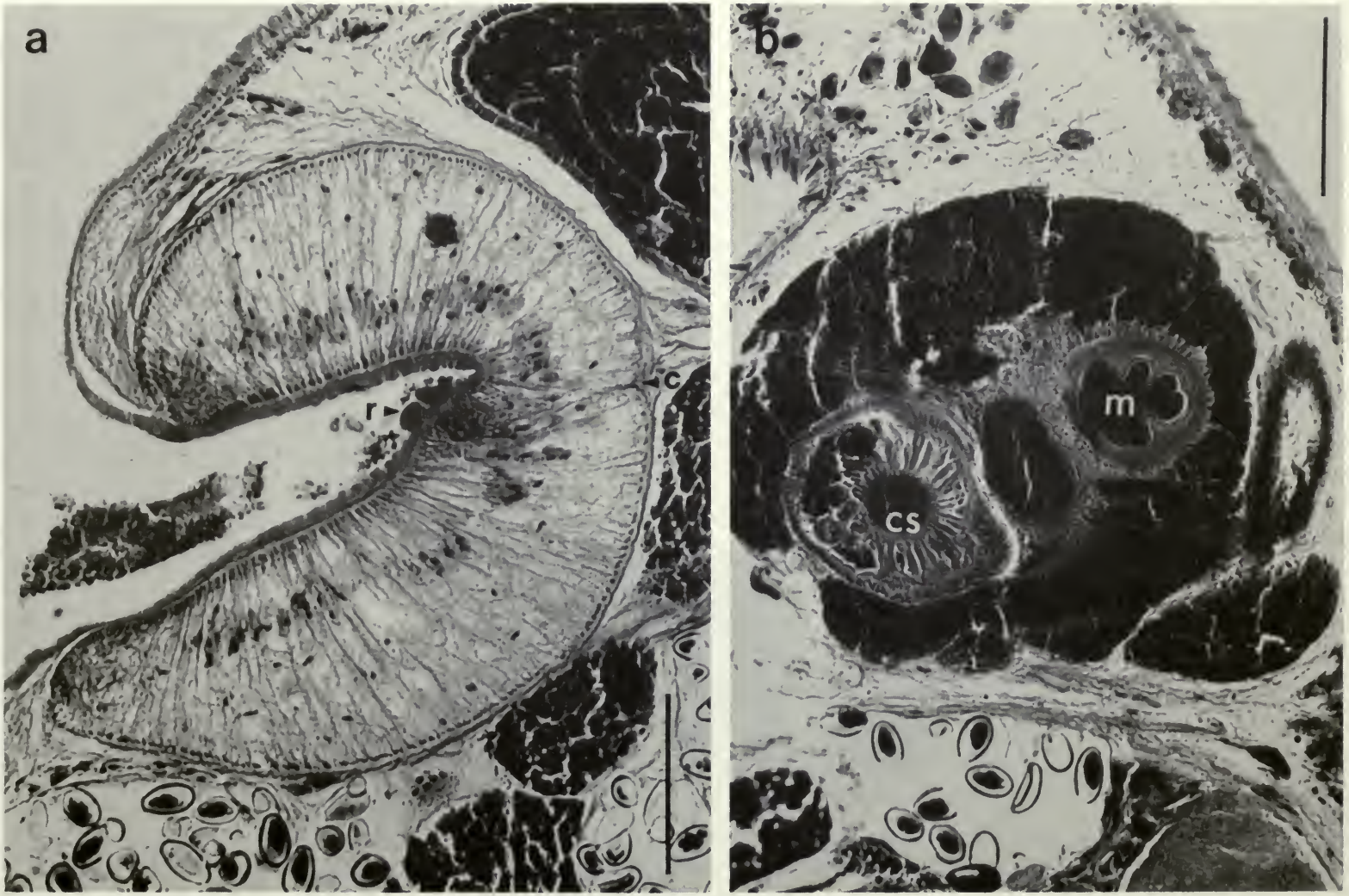

Fig. 25 *Neosteganoderma glandulosum* Byrd, photomicrographs of section of specimen ex *Beryx decadactylus*. (a) Divided ventral sucker showing internal ridge (r) and dorsal cleft (c); (b) Periatrial gland surrounding cirrus-sac (cs) and metraterm (m). Scale bars: a, b 0·1 mm.

seminal receptacle and a narrow, undulating Laurer's canal which opens at about the level of the posterior part of the seminal receptacle (Fig. 24C). The oviduct also receives the common vitelline duct, the vitelline collecting ducts having, apparently, anastomosed close to the oviduct. From Mehlis' gland the *uterus* passes ventrally to fill most of the post-testicular region and the region ventral to the gonads with small, tanned, operculate eggs. The metraterm is a long tube, which, as it approaches the genital atrium, becomes increasingly muscular and develops an internally rugate wall. For much of its length it is ensheathed by an extension of the periatrial gland. It enters the genital atrium through the dorsal wall. The *vitellarium* consists of two lateral fields of about four to eight follicles which lie immediately posterior to the ventral sucker.

Discussion. *Proctophantastes polymixiae* Yamaguti, 1970, from *Polymixia japonica* from off Hawaii is very similar to *N. glandulosum*. Yamaguti (1970) did not compare the two species, but Bray (1973) suggested that they might be conspecific. There appears to be no substantial morphological difference between the species and they have been recorded in closely related hosts although in widely separated geographical areas. Korotaeva's (1982) record of *Neosteganoderma polymixiae* from the zeid fishes *Cyttus novaezealandiae* and *Cyttoidops mccullochi* in the Australia/New Zealand region extends the known distribution of that species, so that at present there seems no good reasons why *N. glandulosum* and *P. polymixiae* should be considered distinct. Examination of the holotype of *N. glandulosum* (USNM 60166) and of the holotype and paratypes of *Proctophantastes polymixiae* (USNM 63568) clearly shows the equatorial division of the ventral sucker.

Genus ***PROCTOPHANTASTES*** Odhner, 1911

Diagnostic features. Body small, pyriform. Caeca reach to level of vitellarium or testes. Ventral sucker large, divided equatorially by dorsal cleft and ventral ridge. Testes symmetrical to oblique in anterior hindbody. Cirrus-sac straight to curved. Seminal vesicle coiled tubular. Pars prostatica wide, vesicular. Ejaculatory duct bears 'spines'. Genital atrium small. Periatrial gland as separated claviform sacs. Genital pore sinistral, marginal; in mid-forebody. Ovary submedian, pretesticular. Uterus mostly post-testicular. Metraterm muscular. Vitellarium two symmetrical, lateral fields of few follicles; pre-testicular; in anterior hindbody. Excretory pore terminal; vesicle elongate saccular. In intestine of marine teleosts.

Comment. Bray (1973), following the work of Manter (1947), considered *Proctophantastes* a synonym of *Steganoderma* Stafford, 1904. He described a 'low muscular ridge' running transversely across the inside of the ventral sucker. Careful observation of serial sections show that the sucker is in fact divided equatorially by this ridge and a narrow, dorsal cleft. This suggests that *Proctophantastes* is very similar to *Neosteganoderma* (whose type-species, at least, has this type of sucker development) and differs only in the simple, unpocketed genital atrium and the weak development of the periatrial gland. The structure of the ventral sucker, however, serves as a useful feature differentiating *Proctophantastes* and *Steganoderma,* thus reversing Bray's earlier decision. The difference between the periatrial gland of *Neosteganoderma* (Fig. 25b) and the small tubular or claviform agglomerations of gland-cells surrounding the genital atrium and metraterm of *Proctophantastes* (Fig. 27c) should be stressed. The periatrial gland is an undivided large mass of gland-cells, possibly delimited by a membranous sac. In contrast, the few gland cells in *Proctophantastes* lie in narrow tubular or claviform membranous packets which are sparsely scattered in the parenchyma.

Proctophantastes abyssorum Odhner, 1911

Deretrema abyssorum (Odhner, 1911) Price, 1934.
Steganoderma abyssorum (Odhner, 1911) Manter, 1947.

Type-host and locality. *Coryphaenoides rupestris*, Trondheim, Norway.

RECORDS

(i) Material studied from the NE Atlantic region

Coelorinchus caelorhinchus [intestine] Northern Bay of Biscay (47°N, 06°W; depth 650 m; Jan., 1971). BM(NH) 1973.5.17.48–50. Material of Bray (1973: 167).

—— [intestine] Southern Bay of Biscay (44°N, 07°W; depth 340–350 m; Jan., 1971). BM(NH) 1973.5.17.48–50. Material of Bray (1973: 167).

—— [intestine] St Kilda, NW Scotland (57°N, 10°W; depth 650–660 m; June, 1974). BM(NH) 1984.2.24.1.

Lepidion eques [intestine] Northern Bay of Biscay (47°N, 06°W; depth 650 m; Jan., 1971). BM(NH) 1973.5.17.51–53. Material of Bray (1973: 167).

—— [intestine] WSW Barra Head, NW Scotland (57°N, 09°W; depth 656–665 m; May, 1973). BM(NH) 1984.2.24.2–4.

Phycis blennoides [intestine] NW of Rona, NW Scotland (60°N, 07°W; depth 900 m; May, 1973). BM(NH) 1984.2.24.5–6.

Rhinonemus cimbrius [intestine] Tjärnö, Sweden. (June, 1971). Material of J. Thulin.

Trachyrincus trachyrincus [intestine] Northern Bay of Biscay (47°N, 06°W; depth 330–650 m; Jan., 1971). BM(NH) 1973.5.17.42–47. Material of Bray (1973: 167).

—— [intestine] Southeastern Bay of Biscay (45°N, 02°W; depth 575–665 m; Jan., 1971). BM(NH) 1973.5.17.42–47. Material of Bray (1973: 167).

—— [rectum] NW of Scotland (58°N, 10°W; depth 1300–1310 m; and 57°N, 09°W; depth 1330–1350 m; Oct., 1978). BM(NH) 1984.2.24.7–9.

(ii) NE Atlantic records from the literature

Coelorinchus caelorhinchus [intestine] Bay of Biscay. Bray (1973: 167).

Coryphaenoides rupestris [posterior intestine] Trondheim, Norway. (1905). Odhner (1911*a*: 238).

Lepidion eques [intestine] Bay of Biscay. Bray (1973: 167).

Melanogrammus aeglefinus [posterior intestine] Trondheim, Norway. (1905). Odhner (1911*a*; 238).

Trachyrincus trachyrincus [intestine] Bay of Biscay. Bray (1973: 167)

ASPECTS OF BIOLOGY. Nothing is known of the life-history of this parasite. It occurs only in gadiform fishes in the north-east Atlantic region and appears to show a predeliction for fishes from the deeper waters, having been found as deep as 1350 m.

PREVIOUS DESCRIPTIONS. Odhner (1911*a*: 238); Bray (1973: 167).

DESCRIPTION (Figs 26, 27). Seventy-two whole-mounts and two sets of serial sections were studied. Measurements are given on Table 14. The worm has a pyriform to elongate pyriform outline (Fig. 26A), with a spinous body-surface in the forebody and most of the hindbody. The subterminal globular *oral sucker* leads to a short, often obscured, prepharynx, a small, globular to slightly oval *pharynx,* and a distinct oesophagus which bifurcates in about the middle of the forebody. The caeca reach to the level of the testes or vitellarium. The *ventral sucker* is distinctive in that it is large, often transversely elongate, and divided equatorially by a ventral muscular ridge and a dorsal cleft (Fig. 27a,b).

The terminal *excretory pore* leads through a narrow duct surrounded by a few gland-cells, into a flattened sac-like vesicle which reaches up to about the level of the testes.

The *testes* are oval to elongate-oval and lie symmetrically or subsymmetrically close to the posterior margin of the ventral sucker. The proximity of the testes to the ventral sucker depends on the degree of contraction of the worm (see Bray, 1973, fig. 7), but they are often separated from the sucker by some of the vitelline follicles. The *cirrus-sac* is large, often recurved, and overlaps the anterior edge of the ventral sucker (Fig. 26B). The seminal vesicle is a coiled tube with the proximal portion occasionally forming a globular sac. It leads into an elongate, vesicular pars prostatica and thence into a muscular ejaculatory duct lined with tegumental rugae and pinnacles. The cirrus-sac also contains numerous gland-cells. The cirrus-sac opens into a distinct, but small, genital atrium which opens on or near the left lateral margin at about the middle of the forebody. Around the genital atrium and distal regions of cirrus-sac and metraterm are tubular to claviform membranous sacs containing gland cells, which may be indistinct (Figs 26A, 27c) or quite well developed (Fig. 26B).

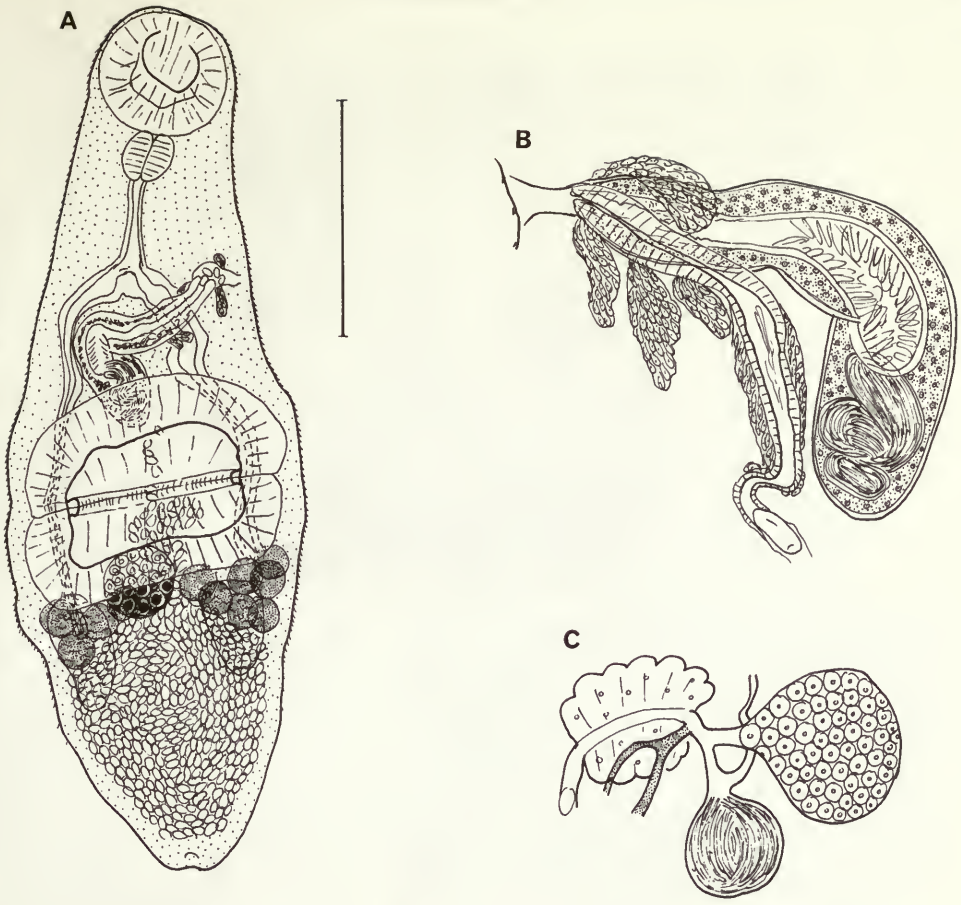

Fig. 26 *Proctophantastes abyssorum* Odhner. (A) Ventral view of specimen ex *Trachyrincus trachyrincus*; (B) Dorsal view of terminal genitalia of specimen ex *Coelorinchus caelorhinchus*; (C) Proximal female genitalia. Scale bar: 0·5 mm.

The *ovary* is more or less globular and lies just antero-medial to the right testis, at the level of the posterior edge of the ventral sucker. From its left side an oviduct passes towards a prominent Mehlis' gland. It receives the common duct from the seminal receptacle and Laurer's canal and the common vitelline duct prior to entering Mehlis' gland. The subglobular, seminal receptacle is often of a similar size to the ovary, posteriorly to which it lies. The duct leading from the oviduct to the seminal receptacle is short, and gives rise to Laurer's canal near its distal end. Laurer's canal passes anteriorly, following a convoluted course and surrounded by gland-cells, to open dorsally just anteriorly to the ovary (Fig. 26C). The common vitelline duct is a slightly enlarged reservoir fed to two narrow collecting ducts. Mehlis' gland lies to the left of the ovary and the *uterus* passes posteriorly from it and fills much of the hindbody. It contains numerous strongly-tanned operculate eggs. The metraterm is muscular and runs beside the cirrus-sac prior to entering the genital atrium dorsally. It is invested for part of its length by a narrow layer of gland-cells. The *vitellarium* consists of two symmetrical clusters of distinct, globular follicles, lying on either side of the body at the posterior margin of the ventral sucker. The clusters consist of 8 to 10 follicles on the poral side and 7 to 9 on the aporal.

Discussion. This species is very similar to the only other member of the genus, *P. gillissi* (Overstreet & Pritchard, 1977) n. comb., which is recorded from the Pacific Ocean. Slight differences in size and sucker-ratio constitute the only morphological differentiating features.

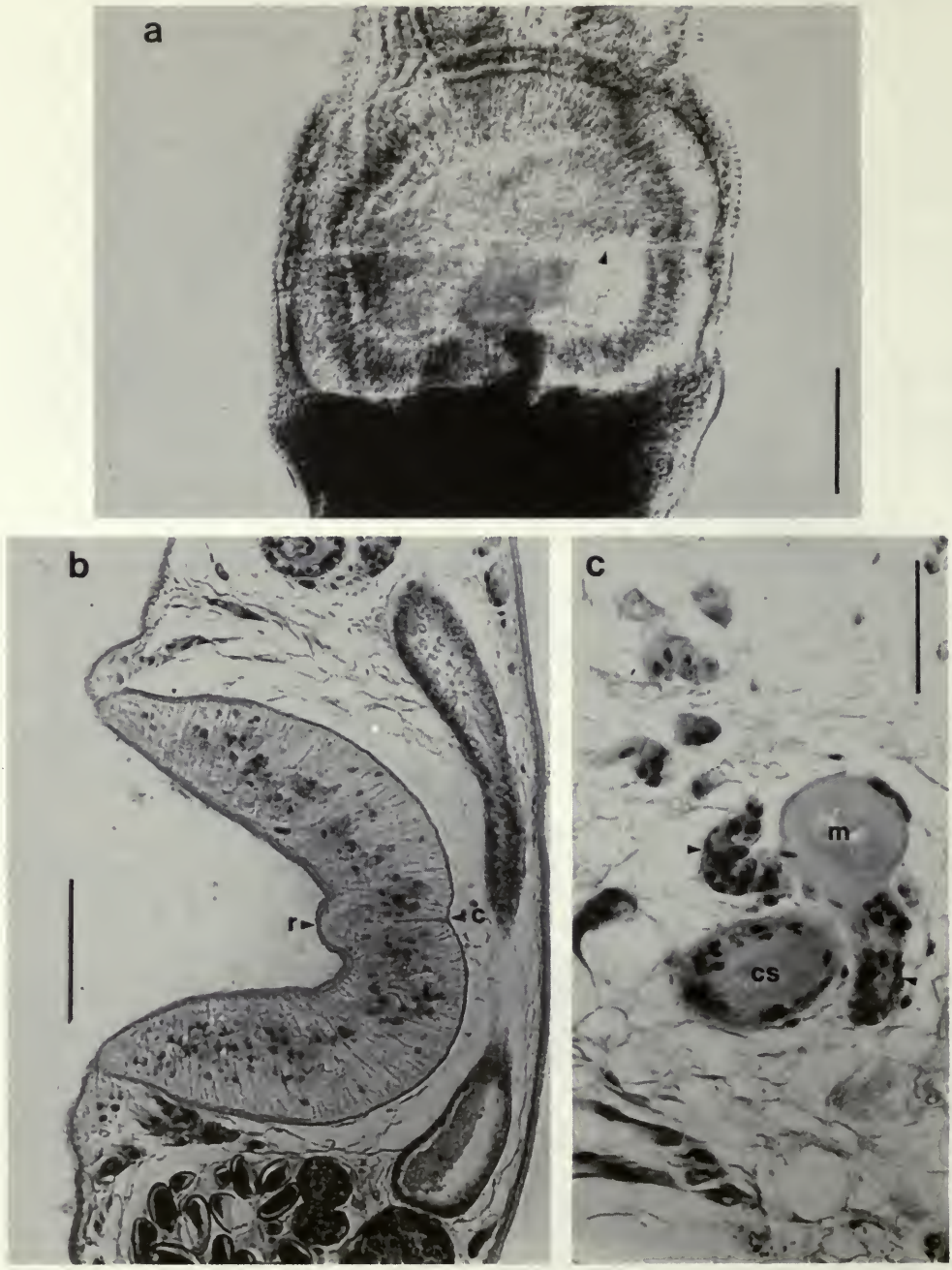

Fig. 27 *Proctophantastes abyssorum* Odhner. (a) Ventral sucker showing division (arrowed), ex *Trachyrincus trachyrincus*; (b) Longitudinal section of divided ventral sucker showing internal ridge (r) and dorsal cleft (c), ex *Phycis blennoides*; (c) Longitudinal section of distal end of cirrus-sac (cs), metraterm (m) and claviform membranous sacs containing gland-cells (arrowed), ex *P. blennoides*. Scale bars: a 0·2 mm, b 0·1 mm, c 0·05 mm.

Table 14 Measurements of *Proctophantastes abyssorum*

Authority	Odhner (1911*a*)	Bray (1973)	Present study
Host	*Coryphaenoides Melanogrammus*	see text	see text
Locality	Norway	see text	see text
Length (mm)	0·8–1·1	0·62–1·66	0·85–1·65
Breadth (mm)	0·35–0·4	0·28–0·63	0·37–0·70
Length : forebody ratio	–	–	1 : 0·34–0·54
Oral sucker (mm)	0·25 diam.	0·18–0·32 diam.	0·15–0·26 × 0·16–0·29
Ventral sucker (mm)	0·35 × 0·45	0·18–0·44 × 0·25–0·60	0·20–0·45 × 0·33–0·63
Sucker-ratio	–	1 : 1·08–2·1	1 : 1·42–3·1
Pharynx (mm)	0·06 diam.	0·03–0·08 diam.	0·05–0·10 × 0·05–0·10
Oesophagus (mm)	1–2·5 × pharynx	0·08–0·22	0·065–0·15
Cirrus-sac (mm)	–	0·2–0·37 × 0·06–0·09	0·28–0·66 × 0·06–0·12
Testes (mm)	–	0·16–0·22 × 0·13–0·20	0·10–0·23 × 0·08–0·12
Ovary (mm)	–	*c.* 0·15 diam.	0·11–0·15 × 0·10–0·12
Eggs (μm)	34–37 × 18	34–31 × 16–21	33–38 × 15–19

Genus ***STEGANODERMA*** Stafford, 1904

Lecithostaphylus Odhner, 1911.
Nordosstrema Issaitschikov, 1928.
Manteroderma Skrjabin, 1957.
Cypseluritrema Yamaguti, 1970.
Steganoderma (Opisthoarchiotrema) Gupta & Sharma, 1974.

DIAGNOSTIC FEATURES. Body oval to elongate-oval. Body-surface spinous. Oesophagus absent to long; caeca reach to testes or beyond. Ventral sucker globular, subequal or larger than oral, sessile or pedunculate. Testes oval, symmetrical to oblique in anterior half of hindbody. Cirrus-sac claviform, straight or curved. Seminal vesicle saccular to elongate, straight or coiled. Pars prostatica vesicular. Genital atrium small. Genital pore sinistral, lateral to sublateral, in forebody. Ovary pre-testicular, usually in hindbody. Eggs tanned. Uterus mainly post-testicular. Vitellarium symmetrical, relatively few (8–16) regular follicles, in lateral regions of anterior hindbody. Excretory pore terminal; vesicle saccular, short to long. Parasitic in intestine of marine teleosts.

COMMENT. Only one species, *S. (Lecithostaphylus) retroflexum,* has hitherto been found in the north-east Atlantic. It may well be that *S. (Steganoderma) formosum* Stafford, 1904 will be found eventually, as it occurs both in the north-western Atlantic and the Barents Sea (Bray, in press *b*).

Steganoderma (Lecithostaphylus) retroflexum (Molin, 1859) Yamaguti, 1953

Distomum retroflexum Molin, 1859.
Podocotyle retroflexum (Molin, 1859) Barbagallo & Drago, 1903.
Lecithostaphylus retroflexum (Molin, 1859) Odhner, 1911.

Steganoderma retroflexum (Molin, 1859) Manter, 1947.
Lecithostaphylus spondyliosomae Fantham, 1938.
Steganoderma spondyliosomae (Fantham, 1938) Manter, 1947.
Steganoderma (Lecithostaphylus) spondyliosomae (Fantham, 1938) Yamaguti, 1953.
Manteroderma spondyliosomae (Fantham, 1938) Skrjabin, 1957.

TYPE-HOST AND LOCALITY. *Belone belone*, Padua, Italy.

RECORDS

(i) Material studied
(a) From the NE Atlantic
Belone belone [intestine] Lisbon, Portugal. BM(NH) 1984.2.29.1.

(b) From elsewhere
Belone belone [intestine] Split, Yugoslavia. Material of O. Sey.
—— [intestine] Zadar, Yugoslavia. BM(NH) 1984.2.29.2.

(ii) NE Atlantic records from the literature
None, but Gijon, Lopez-Roman, De Armas & Valladares (1982) recorded it from the Canary Islands.

ASPECTS OF BIOLOGY. Odhner (1911*b*) believed that *Cercaria thaumantiatis* Graeffe, 1860, from a coelenterate was the larval stage of this species, but it is now considered likely to be the larva of *Lepocreadium album* (Stossich, 1890) (Dollfus, 1925; Palombi, 1931). The great majority of records of this worm are from *Belone belone*, and its possible synonym *Belone acus*, in the Mediterranean Sea. Barbagallo & Drago (1903) recorded it in the flying fish, *Exocoetus volitans*, and Papoutsoglou (1976) listed the wrasse, *Labrus merula*, as a host. Both records are from the Mediterranean. The finding of a worm indistinguishable from *S. retroflexum* in the local sparid *Pachymetopon blochii* in a marine aquarium at Cape Town, South Africa (Fantham, 1938; as *Lecithostaphylus spondyliosomae*), considerably widens the known distribution.

PREVIOUS DESCRIPTIONS Molin (1859 : 290); Odhner (1911*b* : 115); Timon-David (1937*b* : 4); Fantham (1938 : 387).

DESCRIPTION (Fig. 28). Three good specimens and some poorly fixed and fragmentary specimens were available for study. The measurements are given on Table 15. The body has an elongate-oval outline (Fig. 28A), and the surface of these specimens has apparently lost its (usually reported) spines. The globular *oral sucker* opens subterminally leading to a short prepharynx, large globular *pharynx* and a short or practically absent oesophagus. The intestinal bifurcation, which occurs in the mid-forebody, gives rise to narrow caeca which reach into the post-testicular region, usually significantly but often only slightly. The globular *ventral sucker* is borne on a short, protrusible peduncle which may be visible in ventrally mounted preparations as a series of ridges around the sucker. Alternatively it may be deeply withdrawn into the body, but when this occurs clear evidence of the peduncle in the shape of folds around the sucker is apparent. The oral and ventral suckers are of similar sizes. Numerous flask-shaped glandular cells can be seen in the lateral forebody region and reach just into the hindbody.

The *excretory pore* is terminal, but in the specimens available it was not possible to make out the full extent of the vesicle.

The longitudinally elongate, oval *testes* lie symmetrically in the mid-hindbody. The elongate-oval *cirrus-sac*, usually just reaching or overlapping the ventral sucker, contains a claviform, saccular seminal vesicle, a short, vesicular pars prostatica and a short ejaculatory duct, all surrounded by gland-cells (Fig. 28B). It opens into a distinct genital atrium which is surrounded by gland-cells. The genital pore is sinistral, submarginal and at the level of the pharynx or just posterior to it.

The *ovary* is longitudinally elongate oval, lies about half-way between the testes and the ventral sucker, and is separated from the testes by uterine coils. The seminal receptacle and Mehlis' gland lie just posteriorly to the ovary. Laurer's canal opens dorsally at the level of the posterior margin of the ovary. The *uterus*, containing numerous tanned, operculate eggs, fills much of the hindbody. Post-testicularly it reaches close to the lateral margins of the worm, but is restricted pre-testicularly

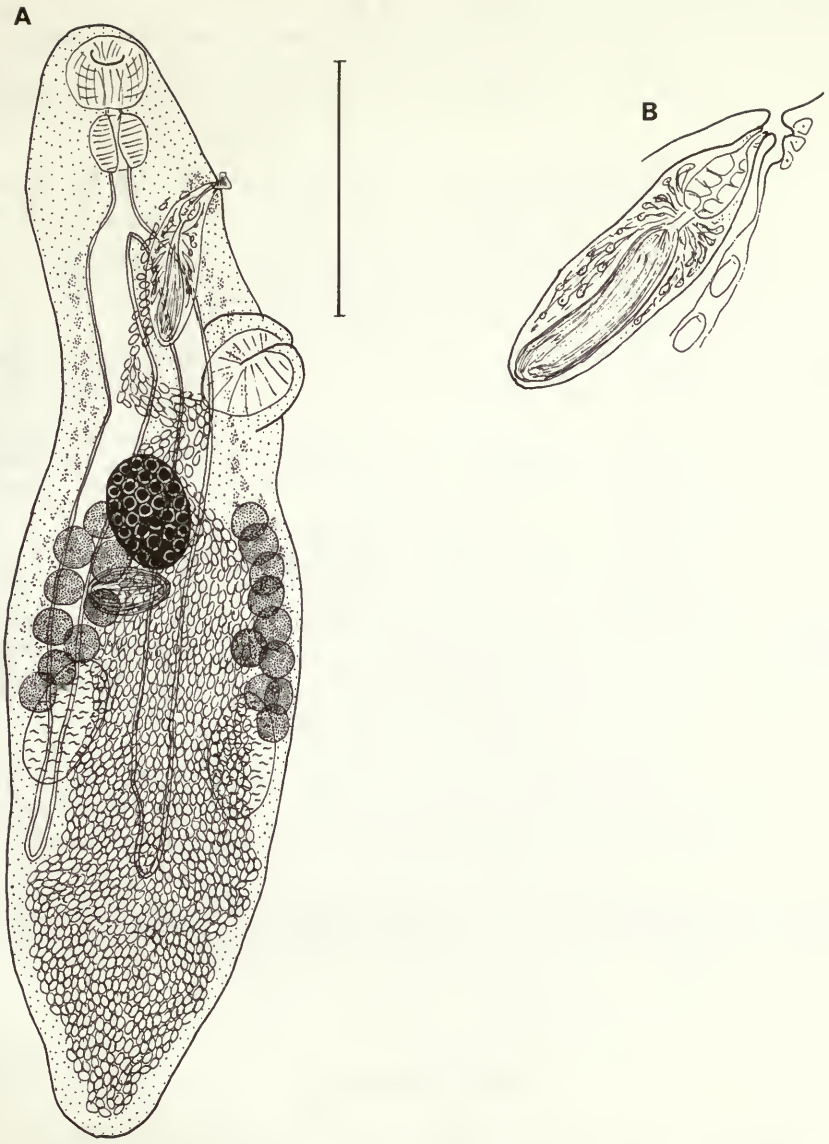

Fig. 28 *Steganoderma (Lecithostaphylus) retroflexum* (Molin). (A) Flattened specimen; (B) Terminal genitalia. Scale bar: 0·5 mm.

to the regions median to the vitelline follicles. The metraterm is weakly developed. The vitellarium consists of two lateral fields of regular follicles arranged 6 to 11 on the poral side and 8 to 9 on the aporal side. Anteriorly the vitelline field reaches from the level of the ovary to the level of the ventral sucker and posteriorly it just overlaps the anterior edge of the testes. The field of flask-shaped gland-cells mentioned above may reach back almost to the posterior region of the vitellarium.

Discussion. *Lecithostaphylus spondyliosomae* Fantham, 1938, is indistinguishable morphologically from *S. retroflexum* and is, therefore, considered a synonym. It is said to differ in having more oblique testes and fewer vitelline follicles. The testes in the figure, however, are precisely symmetrical. This figure, in fact, is very similar to that of *S. retroflexum* in Odhner (1911*b*): they

Table 15 Measurements of *Steganoderma (Lecithostaphylus) retroflexum*

Authority	Odhner (1911*b*)	Timon-David (1937*b*)	Fantham (1938)	Present study	
Host	*Belone acus*	*Belone acus*	*Spondyliosoma blochii*	*Belone belone*	
Locality	Italy	Gulf of Marseille	S. Africa	Portugal	Yugoslavia
Length (mm)	1·5–2·5	2·5	1·42–1·45	2·03	2·01–2·18
Breadth (mm)	0·4–0·55	–	–	0·40	0·38–0·56
Length : forebody ratio	–	–	–	1 : 0·23	1 : 0·24–0·31
Oral sucker (mm)	0·15–0·2 diam.	0·19	0·13 diam.	0·11 × 0·14	0·13–0·14 × 0·13–0·16
Ventral sucker (mm)	0·18–0·23 diam.	0·22	± oral	0·14 × 0·14	0·19 × 0·16
Sucker-ratio	–	–	± 1 : 1	1 ; 1	1 : 1·15
Pharynx (mm)	0·12–0·16 diam.	0·16 diam.	0·08–0·85 × 0·09	0·11 × 0·10	0·10–0·12 × 0·08–0·12
Oesophagus (mm)	–	–	–	–	0·08
Cirrus-sac (mm)	–	0·40	–	0·35 × 0·12	0·26–0·34 × 0·09–0·11
Testes (mm)	–	0·40–0·42 long	0·18–0·195 × 0·10–0·13	–	0·25–0·31 × 0·12–0·17
Ovary (mm)	–	0·17	0·13 diam.	–	0·17–0·22 × 0·11–0·16
Eggs (μm)	38–41 × 20	40 × 20	40 long	36–40 × 20–21	37–41 × 20–25

could almost be of the same specimen. The vitelline follicles as drawn, seven aporal, and nine poral (in *L. spondyliosomae*), fit comfortably within the variation found in *S. retroflexum*.

Host-parasite list

Class Chondrichthyes

Order Lamniformes

Scyliorhinus caniculus (L.): *Diphterostomum betencourti* (Monticelli)
Scyliorhinus stellaris (L.): *Diphterostomum betencourti* (Monticelli)

Order Squaliformes

Squalus acanthias (L.): *Pseudozoogonoides* sp. innom.

Class Osteichthyes

Order Notacanthiformes

Notacanthus chemnitzii Bloch: *Panopula spinosa* (Zubchenko)
Polyacanthonotus rissoanus (Filippi & Verany): *Brachyenteron campbelli* sp. nov.
Panopula bridgeri sp. nov.

Order Salmoniformes

Alepocephalus bairdii Goode & Bean: *Steganodermatoides maceri* sp. nov.

Order Gadiformes

Coelorinchus caelorhinchus (Risso): *Proctophantastes abyssorum* Odhner
Coryphaenoides rupestris Gunnerus: *Proctophantastes abyssorum* Odhner
Lepidion eques (Günther): *Proctophantastes abyssorum* Odhner
Lycodes esmarkii Collet: *Lepidophyllum appyi* sp. nov.
Pseudozoogonoides subaequiporus (Odhner)
Melanogrammus aeglefinus (L.): *Proctophantastes abyssorum* (Odhner)
Phycis blennoides (Brünnich): *Proctophantastes abyssorum* (Odhner)
Rhinonemus cimbrius (L.): *Proctophantastes abyssorum* (Odhner)
Trachyrincus trachyrincus (Risso): *Proctophantastes abyssorum* (Odhner)

Order Atheriniformes

Belone belone (L.): *Steganoderma (Lecithostaphylus) retroflexum* (Molin)

Order Beryciformes

Beryx decadactylus Cuvier: *Neosteganoderma glandulosum* Byrd

Order Zeiformes

Zeus faber L.: *Zoogonoides viviparus* (Olsson)

Order Scorpaeniformes

Myoxocephalus scorpius (L.): *Zoogonoides viviparus* (Olsson)
Taurulus bubalis (Euphrasèn): *Zoogonoides viviparus* (Olsson)

Order Perciformes

Anarhichas denticulatus (Krøyer): *Brachyenteron pycnorganum* (Rees)
Anarhichas lupus L.: *Brachyenteron pycnorganum* (Rees)
Lepidophyllum steenstrupi Odhner
Pseudozoogonoides subaequiporus (Odhner)
Zoogonoides viviparus (Olsson)
Zoogonus rubellus (Olsson)
Anarhichas minor Olafsen: *Brachyenteron pycnorganum* (Rees)
Lepidophyllum steenstrupi Odhner
Pseudozoogonoides subaequiporus (Odhner)
Blennius gattorugine Brünnich: *Zoogonoides viviparus* (Olsson)
Blennius ocellaris L.: *Diphterostomum brusinae* (Stossich)
Zoogonoides viviparus (Olsson)
Blennius pholis L.: *Zoogonus rubellus* (Olsson)
Chelon labrosus (Risso): (?) *Diphterostomum betencourti* (Monticelli)
Diplodus sargus (E. Geoffroy Saint-Hilaire): (?) *Diphterostomum brusinae* (Stossich)
Gobius niger L.: *Zoogonoides viviparus* (Olsson)
Labrus bergylta Ascanius: *Zoogonus rubellus* (Olsson)
Labrus bimaculatus L.: *Zoogonus rubellus* (Olsson)
Pagellus bogaraveo (Brünnich): *Diphterostomum vividum* (Nicoll)
Pomatoschistus minutus (Pallas): *Zoogonoides viviparus* (Olsson)
Trachurus trachurus (L.): *Zoogonoides viviparus* (Olsson)
Zoogonus rubellus (Olsson)

Order Gobiesociformes

Callionymus lyra L.: *Zoogonoides viviparus* (Olsson)
Callionymus maculatus Rafinesque: *Zoogonoides viviparus* (Olsson)
Callionymus reticulatus Valenciennes: *Zoogonoides viviparus* (Olsson)

Order Pleuronectiformes

Glyptocephalus cynoglossus (L.): *Zoogonoides viviparus* (Olsson)
Hippoglossoides platessoides (Fabricius): *Pseudozoogonoides subaequiporus* (Odhner)
Zoogonoides viviparus (Olsson)
Hippoglossus hippoglossus (L.): *Zoogonoides viviparus* (Olsson)
Lepidorhombus whiffiagonis (Walbaum): *Zoogonoides viviparus* (Olsson)
Limanda limanda (L.): *Zoogonoides viviparus* (Olsson)
Zoogonus rubellus (Olsson)
Microchirus variegatus (Donovan): *Zoogonoides viviparus* (Olsson)
Microstomus kitt (Walbaum): *Zoogonoides viviparus* (Olsson)
Platichthys flesus (L.): *Zoogonoides viviparus* (Olsson)
Zoogonus rubellus (Olsson)
Pleuronectes platessa (L.): *Zoogonoides viviparus* (Olsson)
Zoogonus rubellus (Olsson)
Psetta maxima (L.): *Zoogonoides viviparus* (Olsson)
Solea vulgaris (Quensel): *Zoogonoides viviparus* (Olsson)

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